APR 1956
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

PERIODICAL
Marine Biol. Assoc. of the United Kingdom.
Journal.
V.22
1937-38

Volume & DATE OF MAGAZINE | BORROWER'S NAME | TIM

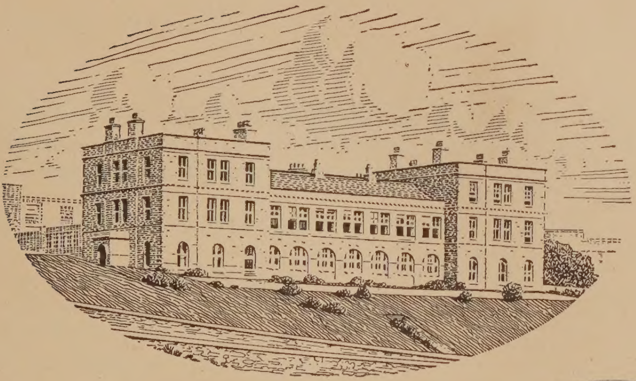
MAY 21 1963

PERIODICAL
Marine Biol. Assoc. of the U. K.
Journal.
V.22
1937-38

LIBRARY
BUR. OF COMM. FISH.
HON. BIOL. LAB.

JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

1678^60



THE PLYMOUTH LABORATORY

APR 1956
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

VOLUME XXII
1937–1938

CAMBRIDGE
AT THE UNIVERSITY PRESS
1938

The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for the accuracy of statements published in this Journal, excepting when those statements are contained in an official report of the Council.

CONTENTS OF VOLUME XXII

NUMBER 1, pp. 1–404, NOVEMBER 29 1937
NUMBER 2, pp. 405–542, APRIL 22 1938

PAGE

Report of the Council:
1936 375

List of Annual Subscriptions paid during the year:
April 1 1936 to March 31 1937 397
List of Donations, 1936–7 399

Income and Expenditure Account and Balance Sheet:
1936–7 400

Obituary:
Edward Thomas Browne, 1866–1937 405

BAYLIS, H. A.
On two species of the trematode genus *Didymozoon* from the mackerel 485

BUTLER, MARGARET R.
See WAKSMAN, S. A.

COLE, H. A.
The fate of the larval organs in the metamorphosis of *Ostrea edulis* 469

COOPER, L. H. N.
Oxidation-reduction potential in sea water 167
On the ratio of nitrogen to phosphorus in the sea 177
The nitrogen cycle in the sea 183

COOPER, L. H. N. and MILNE, A.
The ecology of the Tamar estuary. II. Under-water illumination 509

FORD, E.
Vertebral variation in teleostean fishes 1

GARSTANG, WALTER
On the size-changes of diatoms and their oceanographic significance 83

GOHAR, H. A. F.
The preservation of contractile marine animals in an expanded condition . . . 295

HARTLEY, P. H. T. and SPOONER, G. M.
The ecology of the Tamar estuary. I. Introduction 501

HARVEY, H. W.
Note on selective feeding by *Calanus* 97
The supply of iron to diatoms 205
Note on colloidal ferric hydroxide in sea water 221

JENKIN, PENELOPE M.
Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English Channel 301

LEBOUR, MARIE V.
The newly hatched larva of *Spirontocaris spinus* (Sowerby) var. *lilljeborgi* Danielssen 101
The eggs and larvae of the British prosobranchs with special reference to those living in the plankton 105
The life history of *Kellia suborbicularis* 447

CONTENTS OF VOLUME XXII

Lovern, J. A. and Wood, Henry
Variations in the chemical composition of herring 281

McCance, R. A. and Masters, M.
The chemical composition and the acid base balance of *Archidoris britannica* . . 273

McCance, R. A. and Shackleton, L. R. B.
The metallic constituents of marine gastropods 269

Marshall, S. M., Nicholls, A. G. and Orr, A. P.
On the growth and feeding of the larval and post-larval stages of the Clyde herring 245

Masters, M.
See McCance, R. A.

Milne, A.
The ecology of the Tamar estuary. III. Salinity and temperature conditions in the lower estuary 529
See also Cooper, L. H. N.

Nicholls, A. G.
See Marshall, S. M.

Orr, A. P.
See Marshall, S. M.

Rees, W. J. and Russell, F. S.
On rearing the hydroids of certain medusae, with an account of the methods used 61

Russell, F. S.
The Plymouth offshore medusa fauna 411
On the development of *Muggiaea atlantica* Cunningham 441
On the seasonal abundance of young fish. V. The year 1937 493
See also Rees, W. J.

Shackleton, L. R. B.
See McCance, R. A.

Smith, J. E.
The structure and function of the tube feet in certain echinoderms 345

Spooner, G. M.
See Hartley, P. H. T.

Stokes, J. L.
See Waksman, S. A.

Waksman, S. A., Stokes, J. L. and Butler, Margaret R.
Relation of bacteria to diatoms in sea water 359

Wilson, Douglas P.
The influence of the substratum on the metamorphosis of *Notomastus* larvae . . 227

Wood, Henry
See Lovern, J. A.

Yonge, C. M.
Evolution of ciliary feeding in the Prosobranchia, with an account of feeding in *Capulus ungaricus* 453

ERRATA

Page 101. Line 17, *for* California *read* British Columbia.

,, 111. The figure of *Hydrobia ulvae* (Fig. 2*e*) has in error been drawn sinistral instead of dextral.

,, 112. Line 3, for *Hydrobia ventrosa* read *Hydrobia jenkinsi.*

,, 113. Line 2, for *Calyptraea chinenis* read *Calyptraea chinensis.*

,, 113. Line 11 from bottom, for *R. incospicua* read *R. inconspicua.*

,, 123. Line 30, for *Clelondella* read *Clelandella.*

,, 123. Line 31, for *clelondi* read *clelandi.*

,, 128. 1 line from bottom, for *H. ventrosa* read *H. jenkinsi.*

,, 129. Line 2, for *Hydrobia ventrosa* (Montague) (*H. Jenkinsi*) read *Hydrobia jenkinsi* Smith.

,, 131. After line 2, insert Subgenus *Cingula.*

,, 137. After third paragraph before *Cerithiopsis tubercularis* insert Genus Cerithiopsis.

,, 144. After Family CALYPTRAEIDAE insert Genus Calyptraea. *Calyptraea chinensis* (L.)

,, 146. 2 lines from bottom, for *Nassarius incrassata* read *Nassarius incrassatus.*

,, 150. Line 3, *for* "In *Simnia,* which is one of the true species of *Cypraea* (Cypraeoidea of Schilder)" *read* "In *Simnia,* which belongs to the Cypraeoidea of Schilder".

Also Vol. XXI, No. 2, p. 639, line 4, for *Bathyporeia elegans* read *Bathyporeia gracilis.*

SEP 1954
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

VERTEBRAL VARIATION IN TELEOSTEAN FISHES

By E. Ford, A.R.C.S.
Assistant Director of the Plymouth Laboratory

(Plates I–XVI; Text-figs. 1–18)

CONTENTS

	PAGE
Introduction	2
Material and Methods	2
Nomenclature	3
General Considerations	3
The Form of the Vertebral Column in Relation to Function	5
As a functional neck	5
As the operative base of the caudal fin	6
As support for the median fins	8
In its relation to the form and functioning of the viscera	9
As the housing for the central nervous system	10
As the housing for blood vessels	11
As a seat of attachment for the muscles	12
Its structure in relation to swimming movements	13
The mechanics of the backbone in relation to function	16
Sexual dimorphism seen in vertebral structures	16
Symmetry and Pattern in the Vertebral Column	17
Bilateral symmetry and asymmetry	17
Pattern	18
Estimation of age from bony structures	21
The Number of Vertebrae (n)	22
The determination of (n)	22
The number of vertebrae expressed as $(n)=(a+b+c+\ldots)$	25
The number of vertebrae (n) as the summation of a linear series	27
The degree of constancy in the number of vertebrae	27
in *Clupea harengus*	28
in *Scomber scombrus*	29
in *Caranx trachurus*	30
in *Mullus surmuletus*	32
in *Morone labrax*	32
in *Scorpaena dactyloptera*	33
in *Mugil* spp.	33
The Vertebral Column in Taxonomy and Phylogeny	35
Order Isospondyli	35
Order Anacanthini	39
Order Percomorphi	41
Order Scleroparei	45
Order Heterosomata	47
Order Zeomorphi	50
Order Apodes	51
Order Synentognathi	53
Order Discocephali	54
Order Plectognathi	54
Order Pediculati	56
Concluding Remarks	57
References	57

INTRODUCTION

Since the publication of Heincke's classic treatise on the herring the counting of vertebrae has become a standard operation in the biometric analysis of samples of teleostean fishes taken at random from local populations. But while such routine counting has undoubtedly added greatly to our knowledge of the incidence and magnitude of vertebral variation in a number of economically important species, it has occasioned no little confliction of opinion as to the significance of this variation. Difficulties arising out of my own work on the herring at Plymouth have led me to make a general study of the teleostean backbone in as many species as possible, in an endeavour to learn more of the nature, extent and cause of vertebral variation. After examining over one hundred species, mostly from local waters, I have come to the conclusion that the subject presents a great and varied field of research which is at present but little explored. It would be idle to suggest, therefore, that the present paper should be considered as anything more than an introductory survey of the many problems awaiting detailed investigation. Even so, it may serve to indicate the scope and present position of the Plymouth studies, and prepare the way for fuller work in the future, both at Plymouth and elsewhere.

I have received the greatest assistance from Mr L. S. Wisdom, Laboratory Attendant at the Plymouth Laboratory, whose skill in preparing skeletons for study, and keen interest in all matters relating to the research, I most gratefully acknowledge. I also express thanks to those gentlemen who have from time to time supplied me with needed specimens (see acknowledgements given below). By the courtesy of Dr C. T. Regan, F.R.S., Director of the British Museum (Natural History), I have had access on several occasions to the national collection of fish skeletons at South Kensington, always with the kindly assistance of Mr J. R. Norman, Assistant Keeper in the Department of Zoology.

MATERIAL AND METHODS

As already indicated, most of the fishes examined were obtained locally, either by the research vessels of the Association, or by Plymouth fishing craft landing their catches at the market. Certain species, however, which could not be obtained in this manner, were secured from outside sources. Dr R. S. Clark, Scientific Superintendent of the Fisheries Laboratory, Aberdeen, kindly arranged for material to be sent me from the Aberdeen market; Mr Morley Neale of Messrs Neale and West, Trawler Owners, Cardiff, supplied me with several boxes of fish landed by steam trawlers at Cardiff; the late Mr Howard Dunn of Mevagissey also sent several fishes of interest. Messrs Churchill, Fishmongers, Plymouth, were most helpful in supplying at small cost the "frames" of fishes after they had been filleted. In this way a good number of skeletons of the more expensive kinds of food fishes were secured at no great cost.

As a general rule skeletons were prepared for examination by cooking the fresh fish in water just long enough to loosen the soft tissues from the bones and then teasing and brushing away the flesh, nerves, blood vessels, etc. After some experience of the right length of time for the cooking, no great difficulty was found in obtaining well-cleaned and unbroken skeletons, highly satisfactory for detailed study. One definite advantage of this method of preparation was that the freshly prepared skeleton was still flexible, so that observations could be made regarding the degree of relative movement possessed by the different parts of the vertebral column. When dry, the skeleton could be freely handled and examined in detail. On the other hand, where it was required to give close attention to associated structures such as ribs and fin radials, which are normally attached only by soft tissues, the method was not so satisfactory, and the more lengthy process of dissection and alizarin staining had to be resorted to.

NOMENCLATURE

In the naming and classification of species the *List of British Vertebrates* (Norman, 1935) published by the British Museum (Natural History), has been used, although in some instances, notably species of the Heterosomata, the more familiar synonyms given by Norman have been preferred to the less familiar names which he has adopted.

So far as the naming of skeletal structures is concerned, every endeavour has been made to avoid new terms. No confusion is likely to arise out of the use of such terms as centrum, neural arch, neural spine, haemal arch and haemal spine, and pre- and post-zygapophysis, since these are familiar to all zoologists. It is perhaps desirable to mention that the term *parapophyses* has been applied in a restricted sense to the transverse processes of the pre-caudal (abdominal) vertebrae only. The denotation of the terms epural, hypural, radial and last vertebral segment, in describing the caudal elements of the skeleton is as defined by Whitehouse (1910, p. 592). Mention may also be made of the frequent use of the term *autogenous* as a convenient way of referring to neural and haemal arches which are closely applied to, but definitely not fused with, the vertebral centrum. In freshly prepared skeletons such autogenous processes are easily dissected away from the centra to which they belong.

GENERAL CONSIDERATIONS

Bateson has reminded us in his *Materials for the Study of Variation* that Structural Heterogeneity, Repetition of Parts, Symmetry and Pattern, come near to being universal characters of the bodies of living things. Certainly these are outstanding characters of the vertebral column in the teleostean fish. In its prime construction the column is a jointed rod composed of bilaterally symmetrical segments articulated end to end; but along this axis of symmetry, heterogeneity is expressed by continuous and regular change in form from segment to segment throughout. Orderly, formal change is seen not only in the whole segments but in the homologous parts of the segments, each of which conforms to a distinct "pattern-gradation". All these minor pattern-gradations compound into the major pattern of the vertebral column as a whole.

Structural heterogeneity is clearly related to differentiation of function. In a very real sense, the backbone of a fish is a piece of machinery, so constructed that, as a whole or in its specialized parts, it is capable of performing a variety of functions. Thus, at its anterior end it is designed to make connexion between the head and the trunk and to act as a functional neck in securing independent movement of the head. At its posterior end the backbone is modified to act as the basal support and framework of the caudal fin. Dorsally and ventrally along its length, the backbone gives support to the median fins, while from end to end it provides attachment for the muscles and housing for the central nervous system. In the abdominal region it gives suspension and protection to the viscera, and in the caudal region it conveys the main blood vessels within its haemal arches. Moreover, in the capacity of a flexible rod, the backbone is a vital part of the propelling and turning mechanism by which the fish is enabled to swim and manoeuvre.

The most elementary specification of a backbone which can be given is the total number of segments into which it is divided. This *Number of Vertebrae* (n) is nothing more than an integer, arrived at by counting each segment as of equal and unit value, and has the obvious limitation that it takes no regard for differences in form and function between successive segments. Consequently, it will not distinguish between backbones which, although they agree in (n), are dissimilar in vertebral characteristics other than (n). Alternatively, it will separate backbones which differ in (n), notwithstanding obvious similarities in form-pattern, whether minor or major.

An important advance is made when (n) is expressed as the sum of two or more smaller integers (a), (b), (c), etc., in accordance with the division of the backbone into component parts which are manifestly different in structure. It is now possible to distinguish between, say, $(n)=(a+b+c)$ and $(n)=(a'+b'+c')$. It is also possible to recognize a measure of similarity between, say, $(n)=(a+b+c)$ and $(n')=(a'+b+c)$.

Ultimately it becomes necessary to recognize that the backbone is a series of non-interchangeable segments, each of which has its own exclusive properties of form, function and ordinal position. That is to say, in the last analysis, (n) should be written as the summation of the series (1st + 2nd + 3rd + . . . + nth).

The fuller one is able to make the specification of a backbone the more clear does it become that every backbone is an organ of a particular individual belonging to a particular species. While it is constructed to perform all the essential functions of a backbone as such—and therefore has this much in common with other backbones—it affords evidence of its own identity in every segment throughout its length, as well as in its entirety.

In the pages which follow, observations on backbones of various species are considered in their bearing upon the different matters set out above.

THE FORM OF THE VERTEBRAL COLUMN IN RELATION TO FUNCTION

Perhaps the most obvious character of a fish's backbone is that the form of the vertebral elements changes along the length of the column. This change of form is associated with a change in function. Yet, at the same time, all the vertebrae of the series have something of form in common, since they have common duties to perform. The study of the relationship between form and function is therefore an integral part of an enquiry into vertebral variation, and in this section a review is given of the different functions of the backbone and the associated specializations in the form of the vertebrae concerned.

As a Functional Neck

At its anterior end the backbone is modified to perform the functions which in the higher vertebrates are undertaken by the atlas and axis vertebrae, viz. to form attachment with the skull and to provide a central point about which the head may swing. There is much variation from species to species in the manner and degree in which these two duties are accomplished. The situation in species of the genus *Gadus* is, possibly, a good example with which to commence. Here we find that the first four vertebrae constitute a distinct *post-cranial* section of the vertebral column (Plate II, figs. 1 and 2). Judging by the structure of these vertebrae, the 1st might well be regarded as the equivalent of the atlas, in that it is very securely attached to the skull. For the equivalent of the axis vertebra (as the centre of "head-swing"), however, it seems necessary to pass to the 4th vertebra, regarding the 2nd and 3rd vertebrae as constituting a flexible union between atlas and axis. This means that, with the fish in its normal upright position and the 4th vertebra held stationary, turning of the head to the right or left is made possible by the "flex" union between the posterior end of the 1st vertebra and the anterior end of the 4th. The head is similarly enabled to turn upwards. Oddly enough, however, trials with freshly prepared skeletons, while these were still wet and flexible, showed that the head cannot be bent downwards without rupturing the inter-vertebral ligament.

This suggestion that the four post-cranial vertebrae in the gadoid fish act as a functional "neck" is of interest in connexion with Gray's studies of the swimming and turning of fishes by waves of curvature passing alternately down each side of the body (Gray, 1933*a*, *b*). The matter is considered in greater detail in p. 14.

In the sand-eel (*Ammodytes*) the function of atlas and axis vertebrae, instead of being shared among a number of post-cranial vertebrae as in *Gadus*, appears to be performed by one vertebra only, the 1st. This has a smooth domed-shaped anterior face which fits into a socket at the posterior end of the skull. Conceivably this arrangement is not unconnected with the capacity of the sand-eel to burrow into the subsoil of the sea, in permitting the necessary independence of movement between head and body required for this. A somewhat similar arrangement is found in the conger and the freshwater eel, as well as in the anchovy (*Engraulis*). It would therefore be of interest to determine whether a similar association with a burrowing habit can be demonstrated in these three fishes.

The form of the modified post-cranial vertebrae naturally varies from species to species and will be considered in later descriptions under the different orders, genera and species.

As the Operative Base of the Caudal Fin

While the anterior end of the vertebral column is thus modified to carry the head, its opposite end is specialized to support and operate the caudal fin. Here again a number of vertebral segments are involved in a dual function, for some of these are specially constructed to form the actual basal framework of the fin, whereas others are more concerned in the operation of the fin than in its support.

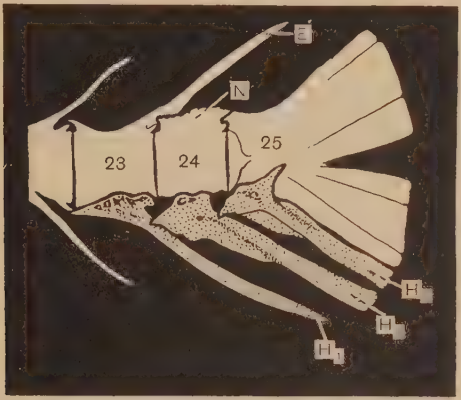
Whitehouse (1910) has given a systematic account of variation in the form of the complex and last vertebral segment in a wide range of species (see also Barrington, 1937). In the present work, therefore, attention has been diverted to the characters of the vertebrae which immediately precede this last or urostylar segment.

In a number of fishes a well-differentiated group of such "tail" segments can be recognized. In the bass (*Morone labrax*), for example, the 23rd and 24th segments (i.e. the antepenultimate and penultimate segments) have a characteristic structure (Text-fig. 1). Ventrally, the haemal spines of both vertebrae are *autogenous**. Dorsally, the neural spine of the 23rd vertebra is elongate and stronger than those immediately preceding, whereas on the 24th vertebra it is reduced to a low-lying crest to the neural arch. These two vertebrae, together with the complex urostylar (25th) segment, thus comprise a well-marked "tail" group of vertebrae, modified for the express purpose of carrying the elements of the caudal fin.

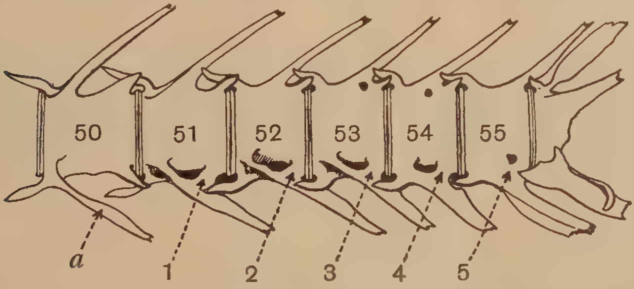
It is to be noted that this particular form of tail base is seen in a wide range of species and, as will be shown later, is a character of considerable taxonomic value. Within the great order Percomorphi, for example, it is of common occurrence, especially in the division Perciformes containing the most generalized forms of the suborder Percoidea (see p. 44). Outside the Perciformes it is seen in full in the Scombroidea (genus *Scomber*) but in a modified form in the Blennioidea and Mugiloidea. Within the order Scleroparei it is again seen in full in the more generalized forms *Scorpaena*, *Sebastes* and *Trigla*. More surprising, perhaps, is that it is typically present in certain species of the Anacanthini, viz. *Merluccius merluccius* (the hake), *Urophycis blennoides* (greater fork-beard), and *Raniceps raninus* (lesser fork-beard). The possible significance of these occurrences in the study of phylogeny will be realized.

---

* The term *autogenous* has been used by Regan. In the present work it is intended to imply that the hypurals are closely applied to, but definitely not fused with, the centrum. In freshly prepared skeletons these autogenous hypurals are easily dissected out of the pockets of the centrum in which they rest. When seen *in situ*, the line of demarcation between hypural and centrum is plainly visible.

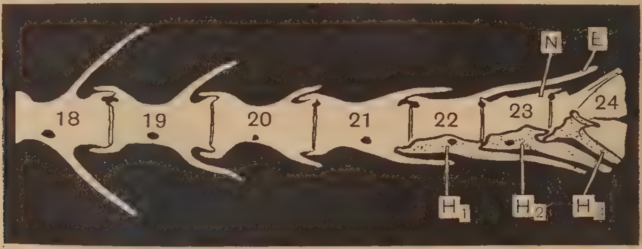


Text-fig. 1. Tail vertebrae of bass (*Morone labrax*). Autogenous hypurals are stippled: *E*, elongated epural of antepenultimate (23rd) vertebra; *N*, crested neural arch of penultimate (24th) vertebra; H_1, hypural of antepenultimate vertebra; H_2, hypural of penultimate vertebra; H_3, anterior, hook-bearing, hypural of terminal vertebra.

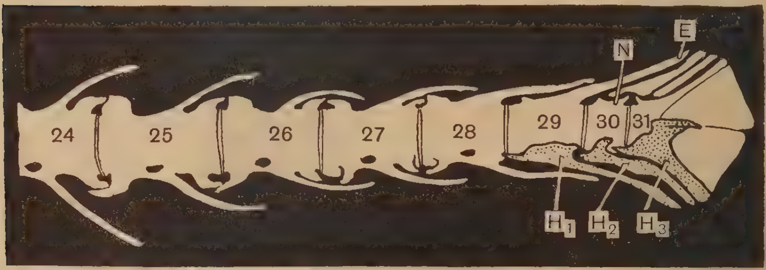


Text-fig. 2. Tail vertebrae of herring (*Clupea harengus*). From Ford (1933, fig. 2 on p. 213). The haemal spines of vertebrae 51–55 are cross-tied to the centrum as indicated by the nos. 1, 2, 3, 4 and 5.

Passing from the vertebrae which form the skeleton of the actual caudal peduncle to those situated immediately in front of them, we sometimes find modification associated with the operation of the caudal fin. Good examples are provided by the herring, scad (*Caranx trachurus*) and mackerel. Previous work has shown (Ford, 1933) that there is in the herring (Text-fig. 2) a well-defined group of from four to eight vertebrae immediately preceding the urostylar segment, and that individual fish with a larger total number of vertebrae in the backbone tend to have a disproportionately larger number of these "tail" vertebrae. In the scad (*Caranx*) the total number of vertebrae in the backbone is normally twenty-four, of which vertebrae 20–24 inclusive form the "tail" group of five segments (Text-fig. 3). In the mackerel (*Scomber scombrus*) the total number of vertebrae in the backbone is normally thirty-one, of which the last six (vertebrae 26–31) comprise the "tail" group (Text-fig. 4). In both the scad and mackerel it cannot be doubted that the specialization in the "tail" section must be considered in association with the organization of the body for active and sustained swimming, in which the tail-end of the body is of the greatest importance. The acme in this type of specialization must surely be the extraordinarily beautiful tail-end of the bonito (*Katsuwonus*), illustrated in Plate IX, fig. 3.



Text-fig. 3. Tail vertebrae of scad (*Caranx trachurus*), comprising vertebrae 20–24 inclusive. For explanation of lettering see Text-fig. 1.



Text-fig. 4. Tail vertebrae of mackerel (*Scomber scombrus*), comprising vertebrae 26–31 inclusive. Lettering is the same as in Text-fig. 1.

As Support for the Median Fins

Seeing that there is much variation in the number, position and form of the dorsal and anal fins among teleostean fishes, we might have expected that the vertebrae from which the fins receive blood vessels and nerves, as well as the neural and haemal spines which support the fin-radials, would also vary accordingly. Yet in numerous instances this is not so, and the backbone remains comparatively undisturbed by fin changes. Thus, in the family Gadidae, although the species present great variety in the number and position of the median fins, the backbone is of the same general form throughout the family, and it is doubtful whether by the examination of the backbone alone one could say very much concerning either the number or position of these fins.

In the percoid fishes, such as *Serranus*, *Mullus*, *Caranx*, *Mugil* and *Labrus*, it is at least possible to see where, in the vertebral series, the first radial of the dorsal fin and the corresponding member of the anal are inserted. In *Caranx*, for example, there is a widening of the interval between the 2nd and 3rd neural spines to make room for the 1st dorsal radial, and a similar widening between the 11th and 12th haemal spines to receive the 1st anal radial (Plate IX, figs. 2 and 4).

In the John Dory (*Zeus faber*) the peculiar "set" of the neural spines of vertebrae 2–8 (Plate XVI, fig. 2), whereby the distal ends of the 3rd and 4th, 5th and 6th, and 7th and 8th, come together, provides accommodation for the dorsal radials. In the boar-fish (*Capros aper*) the 1st dorsal radial, instead of being seated between the 2nd and 3rd neural spines as in the percoid fishes, stands like a peg in a special slot walled in anteriorly by the skull and laterally by the right and left elements of the 1st neural spine. This arrangement is evidently associated with the ingenious mechanism by which the fish is enabled to lock the spines of the dorsal fin in an erected position. Similarly, in the trigger-fish (*Balistes capriscus*) the anterior neural spines are appreciably modified to support the bony framework of the trigger mechanism (Plate XVI, fig. 1).

The dragonet (*Callionymus*) shows modification of the anterior neural spines which, in this genus, must be considered as connected with the marked dorso-ventral compression of the body. The backbone itself does not share in this compression, being, if anything, flattened from side to side rather than dorso-ventrally. To afford accommodation for the anterior dorsal radials, the right and left elements of the neural spines of each vertebra are opened out distally to form forked ends in which the radials stand.

The sucking fish (*Remora remora*) is remarkable for the oval, adhesive disk placed on the broad, flat, upper surface of the head. In order to make room for the skeleton of this disk the neural spines of the first three vertebrae are depressed backwards and downwards to form a low-lying crest to the neural arches.

In its Relation to the Form and Functioning of the Viscera

There is commonly a high degree of specialization in the vertebrae in the abdominal region of the backbone. The pitting of the underside of the centra to house the kidneys, the arrangement of the parapophyses to form a canopy over the air-bladder, the provision of seating for the ribs which encircle the gut; these and other modifications of the abdominal vertebrae to suit the requirements of the viscera are easily observable. Each species necessarily presents its own peculiarities in the abdominal vertebrae.

The proportionate number of vertebrae concerned in these duties is a variate which will be considered later (p. 25), but it may here be noted that the position of the anus in the whole fish is by no means a safe indication of this. In the flat-fishes, for example, the great forward sweep of the bony abdominal bar brings the anus to occupy a position far forward of the last abdominal vertebra. It will also be recalled that the anus in some fishes changes its relative position during the early life of the fish by a process of differential growth of the body (Ford, 1930, 1931 *a*, *b*, concerning the development of the herring, pilchard, sprat and eel). To a greater or less extent the axial skeleton is involved in this disproportionate growth of the body and its organs, more particularly by a change in the form, size and slope of the vertebral processes, with a corresponding alteration of the position of the anus with respect to the vertebrae.

As the Housing for the Central Nervous System

Preceding paragraphs have dealt with the functions performed by localized groups of vertebrae, whereas we must now turn to functions in which each and every vertebra in the backbone takes a more or less equal share. The first of these is the provision of a housing for the spinal cord, namely, the neural canal formed within the neural arches of successive vertebrae. There is much variation from species to species in the form of the neural arches, neurapophyses and neural spines which together form the sides and roofing of the neural canal. Sometimes there is much elaboration in form in one or more of the components, and it will usually be found that each species has recognizably distinct features of its own. Many instances might be given to show how identity can be at once established by a mere glance at, say, the neural spines (cf. *Ammodytes lanceolatus* with *A. tobianus*) or the neurapophyses at their base (cf. *Labrus mixtus* with *L. bergylta*). In the clupeoid fishes and the eels there is a special modification of the neural arches and their processes to form an independent housing for the longitudinal ligament which runs along the length of the column above the spinal cord (see p. 52). Species in general present interesting studies in gradation of pattern in the neural arches and processes from vertebra to vertebra.

But just as each vertebra in a backbone takes its share in housing the spinal cord, so in each provision has to be made for the free passage of the spinal nerves from the spinal cord within the neural canal to the body outside. Very generally the spinal nerves leave the neural canal via foramina in the walls of the neural arches. In the gadoids, however, it is much the more usual for them to leave, not by foramina, but in open grooves between the bases of the neural arches and the post-zygapophyses (Plate III, fig. 2). This applies to all the gadoid genera examined with the exception of *Onos* (the rocklings), and even in the five-bearded rockling, *O. mustelus*, and four-bearded *O. cimbrius*, the spinal nerves leave through grooves instead of foramina. In the three-bearded rocklings, of which there appear to be two species at Plymouth instead of one as formerly supposed, some of the nerves leave via grooves but others through foramina. This is especially interesting because it is a difference between the two forms of three-bearded rocklings at Plymouth in this very character, which (among other evidence) establishes their separate identity. Hitherto, all three-bearded rocklings at Plymouth, as elsewhere in Great Britain, have been referred to the single species *O. tricirratus* (Bloch), but it is now necessary to refer them to two species, the names of which cannot at present be decided. They will be referred to here as form A and form B. In form A the spinal nerves of the 4th to the 12th vertebrae (with an occasional variate) emerge through foramina in the walls of the neural canal, whereas those of the 13th and subsequent vertebrae pass out between the neural spine and posterior zygapophyses (Plate V, fig. 1). In form B foramina are present not only in the anterior vertebrae as in form A, but in the posterior vertebrae as well. The foramina are formed as it were by the fusion of the post-zygapophyses with the base of the neural spines. This difference between these two forms of three-bearded rockling is persistent and well marked, providing one of the best illustrations from present material of the usefulness of vertebral characters for purposes of identification. It is quite another matter to suggest a satisfactory explanation of this difference in terms of function, and I acknowledge my present inability to do so.

As the Housing for Blood Vessels

The housing for longitudinal blood vessels and tracts is a second function of vertebrae in general. It need hardly be said, however, that the haemal arch and its processes not only change greatly in form from vertebra to vertebra along the length of the same backbone, but vary very much from fish to fish. In the caudal region of the body a closed haemal canal is formed by the series of closed haemal arches of the caudal vertebrae. In the gadoid fishes the haemal spines of the anterior caudal vertebrae come together to form much larger loops than those of the posterior ones, whereby a haemal "funnel" is produced into which the hinder end of the air-bladder projects (Plate V, figs 2 and 3). The size and shape of the haemal funnel varies a good deal from species to species and is useful as a clue to identity (see p. 40). In the pre-caudal region of the body there is still more marked divergence in the condition of the haemal arch. In the gadoids a blood tract can be traced along the under side of the centra throughout the length of the pre-caudal region, often as a grooving of the underface of each centrum along the middle line, but in none of the gadoids do the parapophyses come together to form a closed haemal canal. By contrast, in the flat-fishes (Heterosomata) there is a difference in this respect between *Solea* and *Arnoglossus* on the one hand, and the Pleuronectids on the other. In the former the parapophyses come together to form a haemal canal, whereas in the latter they normally remain open, although there may be an occasional weak bridge across the parapophyses of the last one or two pre-caudal vertebrae (e.g. in the lemon-sole, *Pleuronectes microcephalus*). In clupeoids and salmonids (order, Isospondyli) the haemal arches of the posterior pre-caudal vertebrae are transversely bridged to form a closed haemal canal. In the Apodes there is no such bridging in either *Anguilla* or *Conger*, the blood tract running beneath the centra between widely open parapophyses. In the Percomorphi the condition is very different in different fishes. There is a striking contrast, for example, between that of the mackerel (*Scomber*) and that of the bonito (*Katsuwonus*). In the mackerel the first nine or ten pre-caudal vertebrae are quite smooth along their ventral faces and entirely without parapophyses or other processes which might be regarded as housing for the blood system. On the 10th or 11th vertebra, small parapophyses appear which close together at their distal ends to form the first of the closed haemal arches (Plate IX, fig. 1). In the bonito the abdominal vertebrae and their haemal processes show great elaboration to form a housing for a vascular system which is unique among teleostean fishes, as shown by Kishinouye (1923). The blenniiform fishes also provide a good example of variation in allied genera. In the catfish, *Anarhichas lupus*, the haemal arches of the pre-caudal vertebra are all open; in the species of *Blennius* two or three of the hindermost pre-caudals have parapophyses which are transversely bridged to form a haemal canal; in *Pholis gunnellus* all the vertebrae from the 4th onwards have closed haemal arches to form a continuous haemal canal to the end of the backbone. Species of the percomorph family Sparidae (e.g. *Pagellus*, *Box* and *Cantharus*) show a clearly defined blood tract along the middle line of the underside of the centra of the anterior pre-caudal vertebrae. This tract is walled on either side by latero-ventral "flanges" arising from the centra (Plate VIII, fig. 2). Within the order Scleroparei, the gurnards (*Trigla*) show progressive stages in a special modification of the haemal processes of the posterior pre-caudal vertebrae. Thus, in *T. lyra* the 9th to 12th vertebrae each have the distal parts of the right and left haemal arches united to form a flattened, bony disk, so that the blood channel actually lies between the underside of the centrum and the upper side of the disk (Plate XII, fig. 4). It is conceivable that this special modification is to be associated with the size and functioning of the air-bladder, and it is therefore interesting that the flattened disk is most fully developed in *T. lyra* which lives in deeper offshore waters.

As a Seat of Attachment for the Muscles

There is much variation in the "sculpturing" of the outer surfaces of the vertebral centra. Whereas in some species these surfaces are almost unrelievedly smooth, in others they are very irregular and heavily pitted. In the gadoids, eels, and the grey mullets (*Mugil*) it is possible to distinguish species from species by differences in this respect (cf. figs. 2 and 3 in Plate XI).

Mention of the grey mullets brings to mind the curious hook-like processes which project posteriorly from either side of the neural arch of the 2nd vertebra, immediately behind the parapophyses (Plate XI, fig. 1), and which have not been observed in any other genus of fishes examined at Plymouth. The exact function of these processes is obscure, unless they have to do with the attachment of muscles. In a number of species, including the gar-fish (*Belone*), the conger, and certain of the flat-fishes, lateral apophyses, projecting from the centra on either side in the middle line, also appear to function as skeletal supports for the muscles. They form a series which is quite distinct from either the rib-bearing parapophyses or the haemal processes. Their presence in the caudal region in the conger, but absence in the fresh-water eel, forms a reliable distinction between the two eels (Text-fig. 16 on p. 52). In the flat-fishes it is usual to find them more strongly developed on the "upper" (eyed) side than on the "lower" (blind) side (Plate XIV, fig. 3). In the Pleuronectidae and Bothidae (with the exception of *Arnoglossus*) they are confined to the caudal vertebrae—or, possibly it would be more correct to say that in the pre-caudal vertebrae they become merged into the parapophyses—while in *Arnoglossus* and the Soleidae the series is distinct and continuous throughout the length of the vertebral column (Plate XIII, fig. 3). These lateral apophyses are, therefore, of considerable aid in the recognition of families, genera and even species.

Its Structure in Relation to Swimming Movements

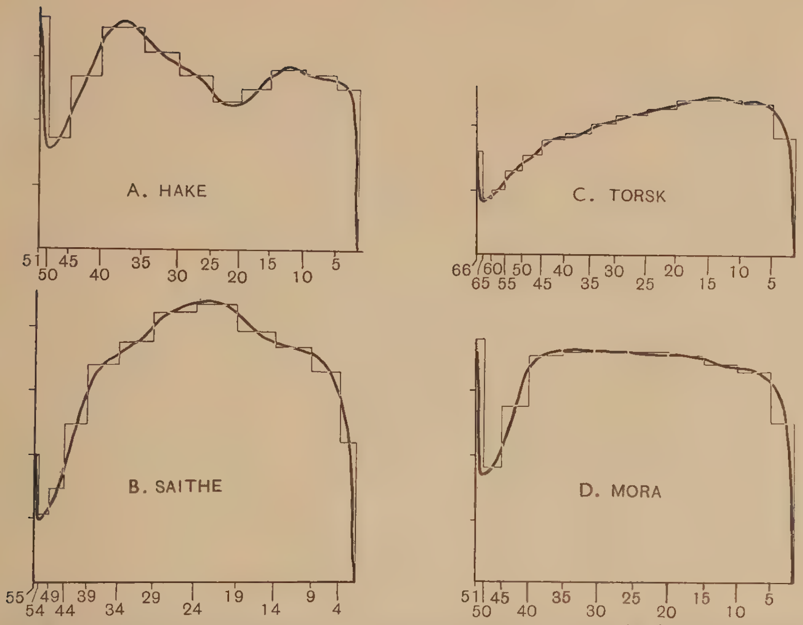
Gray (1933*a*) has demonstrated that although the swimming motions of various types of fish, as observed by the human eye, appear to vary considerably from one species to another, they agree in being the result of waves of curvature passing along the body with increasing amplitude as the hind end of the fish is approached. The only significant differences between the swimming of the eel and that of the mackerel, for example, are the relatively larger amplitude of the waves towards the anterior end of the body and the larger length of wave in the eel. The study of the vertebral column in relation to swimming, therefore, amounts to a study of its flexibility. Now we know that provision for flexure is afforded by the ligamentary articulations between the rigid vertebrae, and we may conclude that the nature and extent of spinal flexure is governed by three factors: viz. (1) the number of articulations, (2) their disposition along the length of the vertebral column, and (3) the amount of flexure procurable at each. It is easily seen that these governing factors may be expressed in terms of the solid vertebral structures instead of the elastic articulations between the latter. Thus, the number of articulations is a function of the number of vertebrae, the disposition of the articulations is expressible in terms of the length of each vertebra, while the amount of flexure procurable at each articulation is largely dependent upon the extent to which successive vertebrae are interlocked by dorsal and ventral processes.

In the present consideration, however, it is hardly possible thus to consider the vertebral column apart from the cranium and caudal fin, since the three are flexibly united. As the fish swims, the head swings alternately right and left of the path along which the fish is moving, acting like a rigid rod of relatively great length swinging from the anterior end of the vertebral column through the medium of a flexible union. Meanwhile, at the opposite end, the caudal fin is operating as a surface which offers high resistance to transverse movement of the body (Gray, 1933*a*, p. 18). Between these two, the vertebral column itself takes up curvature within the limits imposed by its own inherent properties of flexibility and in harmony with the head swing and tail inhibition.

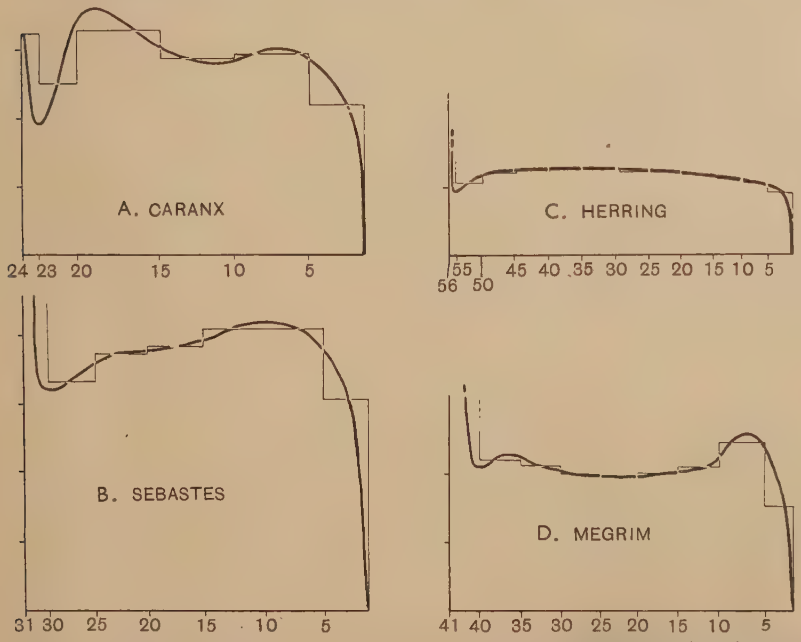
In the third place it has to be remembered that the backbone is embedded in a fleshy body within which it operates in response to waves of muscular contraction. Ultimately, therefore, it becomes necessary to take into account the nature and form of body as a further factor governing the action of the backbone in swimming movements.

During the course of the general survey with which this paper deals it has not been possible to make a detailed study along the lines indicated above. Nevertheless, there are some relevant observations which may be conveniently referred to at this stage. Reference has already been made to vertebral length as one factor governing the nature and extent of spinal curvature, and it may now be pointed out that fishes differ to a marked degree in the manner in which the length of the vertebral column is distributed among the component vertebrae. Not only are the vertebrae of the individual fish unequal in length, but the "gradient" of vertebral length along the column differs from fish to fish. This is demonstrated in the graphs shown in Text-figs. 5 and 6, where differences in the position of the longest vertebrae, and in the relative lengths of corresponding segments of the column are self-evident. It will be observed that in some fishes (e.g. hake, Text-fig. 5A, and *Caranx*, Text-fig. 6A) there is a marked tendency towards bimodality in the graph. This tendency is shown very commonly among flat-fishes of the order Heterosomata.

Some attention has also been given to the structure and action of the union between vertebral column and cranium. On p. 5 of this paper, the four anterior vertebrae in species of *Gadus* were treated as the functional equivalent of the atlas and axis vertebrae of the higher vertebrates in forming the actual attachment between vertebral column and cranium, and making the necessary provision for head-swing. Now this is of direct interest in connexion with Gray's studies of the swimming fish. Gray has shown how each segment of the body moves forward along a sinusoidal path transverse to the axis of forward movement, and from a figure which he gives of superimposed tracings of the left side of a butterfish showing the passage of a complete swimming wave (Gray, 1933*a*, fig. 5A), it is seen that the amplitude of this transverse displacement of the body is least at a point lying a short distance behind the junction of head and body. This suggests that, in the gadoids, the 4th vertebra may mark the position of minimum transverse displacement. The distance



Text-fig. 5. Graphs showing variation in length of vertebral centrum in Gadoid backbones. The base-line is divided according to the length of successive sections of five vertebrae. The values of the ordinates are proportional to the average length of centrum in these sections: A, hake (*Merluccius merluccius*); B, saithe (*Gadus virens*); C, torsk (*Brosme brosme*); D, *Mora mediterranea*.



Text-fig. 6. Graphs similar to those of Text-fig. 5 for the following species: A, *Caranx trachurus*; B, *Sebastes marinus*; C, *Clupea harengus*; D, *Lepidorhombus whiff-iagonis*.

from the tip of the snout to the middle of the 4th vertebra, compared with the total length of the body, might therefore prove of some significance in determining the particular form of the swimming wave exhibited by a gadoid fish.

Turning to the tail-end of the body it is of interest to follow up Gray's illustration of the way in which the caudal fin works (Gray, 1933*a*, p. 18). He compares the effect of the fin to that produced by attaching a flat plate to the distal end of a steel wire and oscillating the proximal end of the wire through a small angle. Without a flat plate each part of the wire moves in practically the same phase as any other part, but when the plate is present the distal end of the wire lags behind the proximal end. With the plate, a series of movements is set up which is strikingly similar to the normal movements of a fish's body; without the attached plate the movements are comparable to those of a fish from which the tail fin has been removed. Pursuing Gray's analogy, the terminal portion of the vertebral column, in forming the base of the caudal fin, may be likened to the beating out of the distal end of the steel wire to form a firm place of attachment for the plate. As such, it is neither entirely wire nor entirely plate, but a combination of the two. That is to say, the "tail" vertebrae will have something in common with the "body" vertebrae in transmitting swimming waves of curvature, but will also be concerned in the working of the caudal fin to produce lag. Variation from species to species in the "tail" group of vertebrae, to which reference has already been made in p. 6, should therefore provide much useful material for study.

The Mechanics of the Backbone in Relation to Function

This survey of the backbone as a piece of machinery would not be complete without some consideration of the backbone from the point of view of the engineer. Although a detailed study of this nature could only be conducted by a fully qualified investigator, no specialized knowledge is needed to appreciate the richness of the research material available to such an investigator. In the texture of the bone of which the vertebrae are constructed; in the provision against stresses and strains set up at different points; in the arrangement of processes to facilitate co-ordinated action of the vertebrae; in the modification of successive vertebrae for special functions; in the general matter of economy of materials; in these and many other problems, every species presents its own characteristics.

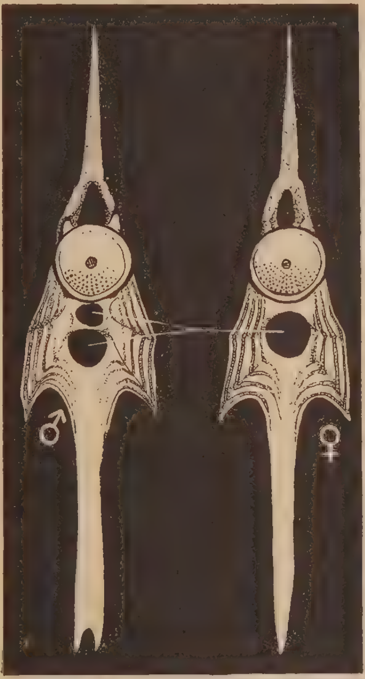
Sexual Dimorphism seen in Vertebral Structures

Although in the present work no very special attention has been given to possible difference between the sexes, the situation in the wrasses is worthy of mention. It is known that the male and female of *Labrus mixtus* differ appreciably in outward appearance. Internally, the backbone is much the same in both, except that there is a marked difference in the relative size of the circular haemal canal of the first caudal vertebra, this being larger in the male than in the female. In *Labrus bergylta* the corresponding canal is normal in the female but appears to be duplicated in the male, at least in the few specimens which it has been possible to examine at Plymouth (Text-fig. 7).

Symmetry and Pattern in the Vertebral Column

Bilateral Symmetry and Asymmetry

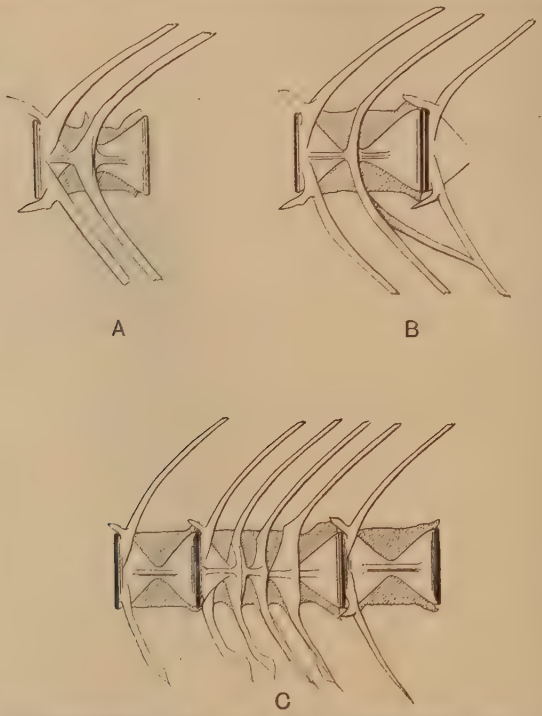
Symmetry and pattern are phenomena which are at once discernible in the teleostean backbone. Dealing first with symmetry, the majority of species exhibit bilateral symmetry in their backbones because the latter are built up of segments which are themselves bilaterally symmetrical. In the flat-fishes (Heterosomata), however, in which the original right and left sides of the body have become functional upper and lower surfaces, this symmetry is more or less disturbed according to species, and the right and left halves of the vertebrae are no longer quite alike (see Cole & Johnstone, 1901, and Kyle, 1926). This is particularly noticeable in the lateral apophyses of sinistral species such as the brill, megrim, scaldback and topknot, which are decidedly more strongly developed on the upper (coloured) side than on the lower (blind) side (Plate XIV, fig. 3). Outside the order Heterosomata, bilateral symmetry is fairly uniformly preserved in the backbone as a whole, but it is apt to break down in individual vertebrae. This occurs most commonly at points along the backbone where there is normally a fairly sharp change in vertebral form. Adopting the nomenclature of Bateson (1894, p. 85), these are cases of *homoeosis*. That is to say, they are cases of one vertebral segment partially assuming the form proper to its neighbour in front or behind. For example, in the typical gadoid backbone there is a sharp change in form between the last of the abdominal vertebrae and the first of the caudals, the former having widely open parapophyses, and the latter a closed haemal arch forming the first element of the "haemal funnel". Not infrequently, however, it will be found that between the typical abdominal vertebrae and the typical anterior caudals there is a transitional form of vertebra which on the one side exhibits



Text-fig. 7. *Labrus bergylta*. Sexual difference in the condition of the haemal arch of the 1st caudal vertebra. In the male there are two canals, but in the female one only.

the characters of an abdominal vertebra, and on the other side the characters of a caudal vertebra.

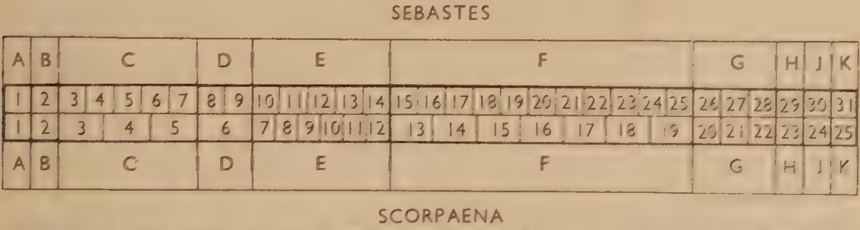
Anatomical differences between the two sides of one and the same vertebra are very common in the herring and other allied clupeoids. Sometimes a vertebral centrum will show incipient division into two or more parts on the one side only; or there may be duplication of the neural and haemal spines on one side, while the other side is normal. Text-fig. 8 B shows an example of another kind of bilateral irregularity in the haemal arch of the herring. Further attention to this phenomenon will be given at a later stage in this paper (see p. 28).



Text-fig. 8. Abnormal vertebrae in the herring. From Ford & Bull (1926). A, 33rd vertebra of a herring 29 cm. in length; B, 21st vertebra of a herring 22 cm. in length; C, fusion of vertebrae 25–28 inclusive in a herring 28 cm. long; vertebrae 24 and 29 are normal.

Pattern

Turning from symmetry and asymmetry to pattern, the teleostean backbone presents much interesting material for the study of gradational change in the form of homologous parts along the length of the column, and in the composite pattern of certain sections of the backbone and of the backbone as a whole. It is hardly an exaggeration to say that every structural feature of a vertebral segment, even to the smallest zygapophysis, forms one unit of a discrete gradation series, and that the natural compounding of these series gives to the backbone as a whole a pattern which is distinctive of the species to which the backbone belongs. Furthermore, after comparing species with species, it is impossible to escape the impression that phylogenetic relationship is made manifest by agreement both in the characters of the individual gradation series and in their compounded pattern. The suggestion is that all gadoid backbones conform to a gadoid pattern, all clupeoids to a clupeoid pattern, and so on. And each of these patterns will have its own distinctive set of gradation series. An excellent example of this is provided by the backbone of the shad, *Alosa alosa*, described in detail on p. 36.



Text-fig. 9. Comparison between the backbones of *Scorpaena dactyloptera* and *Sebastes marinus* (see Pl. XII, figs. 1 and 2). Each backbone has been divided into sections A to K according to the characters enumerated below, and the serial numbers of the vertebrae in the successive sections in the two species are shown in the diagram: A, vertebra 1 which bears autogenous neural spines; B, vertebra 2 in which the neural spine is of the same height as that of vertebra 1 and brought into adjacency with the latter; C, vertebrae without prominent parapophyses; D, vertebrae with well-developed and open parapophyses; E, vertebrae with closed and fenestrated haemal arches; F, anterior caudal vertebrae in which the haemal arches are not normally fenestrated; G, caudal vertebrae with fenestrated haemal arches; H, antepenultimate vertebra with elongate epural and autogenous hypural; J, penultimate vertebra with crested neural arch and autogenous hypural; K, **terminal vertebra with anterior, autogenous and hooked, hypural.**

It may next be observed that formal pattern in the backbone is not necessarily dependent upon the number of segments of which the backbone is composed. Theoretically, at any rate, any basic pattern, compounded of a given set of gradation series, may be spread over a large total number of segments or a small one. Alternatively, one or more parts of the pattern may be distributed over a larger or smaller number of segments. In both instances, an increase in the number of segments results simply in a corresponding reduction in the amount of structural difference between successive segments. In illustration it is of interest to compare the backbone of *Sebastes marinus* in which there are thirty-one segments with that of *Scorpaena dactyloptera* in which there are only twenty-five. There is an obvious similarity of pattern between the two backbones, the extent of which may be gathered from Text-fig. 9 in which regions along the two columns which are comparable in structure are brought into adjacency. It is not argued from this comparison that

Text-fig. 9 depicts a table of individual homologies between the vertebrae of *Sebastes* and those of *Scorpaena*, but rather that the same basic pattern is present in the two species, despite a difference in the total number of vertebrae over which it is spread, and the manner in which it is spread. In other words, the interest of the comparison centres in the mutual conformity to a single pattern, and not in the ordinal positions of vertebrae which correspond in structure.

Another illustration is provided by the varying form of the caudal peduncle in the gadoid fishes. It is characteristic of the gadoid that a considerable number of vertebrae directly support rays of the caudal fin. In the ling (*Molva molva*), for example, no less than thirteen vertebrae function in this way (Whitehouse, 1910). But the number of vertebrae, their relative length, and also the slope and length of the neural and haemal spines which bear fin-rays, all vary from species to species. Yet there can be no denying that there is a common ground plan on which all the tail bases are constructed (Plate VI).

The application of principles described by D'Arcy Thompson in his *Growth and Form*, chapter XVII, is also very appropriate to the study of pattern in the backbone. It will be recalled that D'Arcy Thompson gives striking instances of the effect of redrawing the outline of a fish on an alternative set of co-ordinates. Thus, when the outline of *Argyropelecus olfersi*, drawn to Cartesian co-ordinates, is transferred to a system of oblique co-ordinates whose axes are inclined at an angle of 70°, the new figure is a close approximation to the form of the allied fish, *Sternoptyx diaphana*. Now, turning to the backbone, it is easy to think of the neural and haemal spines as a series of natural "y" axes, set at intervals along a natural "x" axis following the middle line of the vertebral column, and about which the organs of the body are orientated. Obviously, there are three factors which govern the overall form of a body thus orientated:

(1) The disposition of the neural and haemal spines along the vertebral column (i.e. the distances along the "x" axis at which the "y" axes are erected). This is, of course, dependent upon the number and individual lengths of successive vertebrae.

(2) The slope of the neural and haemal spines (i.e. the angles which the y axes make with the x axis).

(3) The length of the neural and haemal spines (i.e. the values of y as measured from the x axis along the y axes to the distal ends of the spines).

(4) The degree of departure from a straight line of the long axis of the backbone (i.e. the x axis).

A change in any one of these four factors will obviously alter the form both of the backbone itself and of the body orientated about it, despite the fact that the number of vertebrae and the manner in which the various parts of the body (including the median fins) with respect to the vertebrae remain unaltered meanwhile. It need occasion no surprise, therefore, that many species which differ markedly in outward form are found to have backbones which can be regarded as little more than "distortions" of a basic, generalized "type". In each of the orders represented in the Plymouth material there is abundant evidence of this, presenting opportunity for research of an exceptionally interesting nature. It need hardly be added that variation from basic "type" may be more pronounced in one part of the backbone than in another, each species exhibiting its own characteristics in this respect.

Estimation of Age from Bony Structures

Although the estimation of age hardly comes within the scope of the present work, some incidental observations concerning it which have been made from time to time during the steady examination of skeletons may not be out of place. As is well known, a highly specialized technique has been developed for "reading" the age of certain fishes from their scales or otoliths. There are many species, however, in which such proven clues to age are not as yet established. There is, of course, nothing new in the fact that the bones of the skull and vertebral column frequently show "growth rings". Such rings have been observed in a number of the cleaned and dried skeletons in the Plymouth material, although it is not at present possible to give a definite statement that they are "annual" rings, or even that they can be relied upon as indices of age. Detailed study could alone determine this.

In the bass (*Morone labrax*) the supra-occipital exhibits growth zones of a remarkable clarity (Plate VII, fig. 2). The supra-occipital in *Serranus cabrilla* is similarly marked (Plate VIII, fig. 1). In the grey mullets (*Mugil*) growth rings are visible on the parapophyses of the 2nd to the 5th vertebrae. In the wrasses (e.g. *Labrus bergylta*) the rings are often very distinct on the posterior parapophyses and on the expanded base of the 1st caudal haemal spine (Plate X, fig. 1). Among the flat-fishes (Heterosomata) (Plate XV, fig. 2) the bones of the last vertebral segment are flattened plates, and are well worth study in this respect. In the John Dory (Plate XVI, fig. 3), certain of the skull bones are zoned. It is also known that the concave ends of the vertebral centra often show growth rings quite distinctly. This has been observed especially in elasmobranch fishes, and may well prove to be of practical use. Among gadoid fishes, growth rings show up rather well in the haddock and ling on the parapophyses, and in the skull bones of *Mora*. Generally speaking, growth rings and zones are rendered clearer by examination on a black background under water.

The Number of Vertebrae (*n*)

The *number of vertebrae*, defined as an integer, indicating how many segments there are in the linear series of a vertebral column, would seem to be a readily understood and easily determinable character. Certainly it is one which is very generally given in systematic works on fishes, and extensively employed in biometric investigations of fishable populations of herring, cod, plaice and other food species. There is a great literature on the variation in the number of vertebrae and on its dependence upon heredity and environment. It is, therefore, a character about which knowledge should be as full as possible.

The Determination of (*n*)

In the practical determination of (*n*) there is normally no difficulty in the actual counting, provided that backbones are sufficiently well exposed to the view of the counter. Beginning with the 1st vertebra and counting one for each bony segment behind it, including the complex terminal, or urostylar segment, the total (*n*) is easily and correctly determined. Sometimes, however, and with a frequency dependent upon the species under study, the count presents difficulty. The most obvious case of this kind is that of a backbone having one or more abnormally long and irregularly formed segments, which suggest local fusions of adjacent vertebrae (Text-fig. 8). If these non-typical segments are counted as if they were single vertebrae, the total (*n*) for the backbone proves lower than the normal mean. Ford & Bull (1926) have shown that, in the herring, the normal value of (*n*) is restored if the irregular segments are considered as fusions of vertebrae and therefore counted as such. More recently, Schnakenbeck (1931) and Kändler (1932) have published data to the same effect.

There is a second type of complex vertebral segment which is not so easily evaluated. The essential features are the undivided, although often elongate, centrum, and the duplication of vertebral processes. Sometimes the neural spine is duplicated, and at others the haemal, but quite frequently both neural and haemal are duplicated (Text-fig. 10). Duplication may occur on both sides of the body, or (less frequently) on one side only. Details on the structure and occurrence of such segments in the herring and species of flat-fish are given by Ford (1933) and Kändler (1932).

In all species examined by the writer at Plymouth, save one (*Morone labrax*), segments of this character have been situated towards the caudal end of the vertebral series. In the clupeoids, e.g. in the herring, pilchard and sprat, duplicated processes occur on either or both of the two vertebrae immediately preceding the last or "urostylar" segment; in the gadoids they are confined to the vertebra next but one to the terminal segment, and in flat-fishes (Heterosomata) to the vertebra immediately preceding the terminal segment. Kändler, however, records extensive duplication of the neural spine of the 1st vertebra in the flat-fishes, but this has not been seen in the Plymouth material, despite a careful look-out for the possibility. Oddly enough, of the two solitary cases of this kind of duplication on the 1st vertebra, which have been observed at Plymouth, both occurred in the bass (*Morone labrax*). Complex segments at the posterior end of the backbone are very widespread and have been seen in the following species:

Order Isospondyli: *Clupea harengus, C. sprattus, Alosa alosa, Sardina pilchardus, Engraulis encrasicholus, Salmo trutta, Argentina silus.*

Order Anacanthini: *Gadus callarias, G. aeglifinus, G. luscus, G. minutus, G. merlangus, G. pollachius, G. poutassou, Urophycis blennoides, Molva molva, M. elongata, Mora mediterranea, Onos mustelus.*

Order Percomorphi: *Cepola rubescens, Ctenolabrus rupestris, Centrolabrus exoletus, Ammodytes lanceolatus, Atherina presbyter.*

Order Heterosomata: *Arnoglossus laterna, Rhombus maximus, Lepidorhombus whiff-iagonis, Phrynorhombus norvegicus, P. regius, Zeugopterus punctatus, Hippoglossoides platessoides, Pleuronectes limanda, P. platessa, P. flesus, Solea solea, S. lascaris, S. variegata.*

As shown by this list, the complex segments are of quite general occurrence in the Isospondyli, Anacanthini and Heterosomata. They are far less common in the Percomorphi and Scleroparei, however, and have not been observed in *Serranus cabrilla, Morone labrax* (except for two specimens), *Caranx trachurus, Mullus surmuletus, Scomber scombrus* and *Scorpaena dactyloptera*, although numerous backbones of each of these species have been examined. In a corresponding number of clupeoids, gadoids or flat-fish, there would certainly have been several occurrences of complex segments. Perhaps this is hardly surprising in view of the great degree of stability in the number of vertebrae and general form of the vertebral column in the species of Percomorphi and Scleroparei concerned.

In only a small number of species has the material for study been sufficient to estimate the frequency with which complete segments occur, but the data collected is at least sufficient to show that the frequency is sometimes very appreciable:

Species	Total no. of specimens examined	Specimens with complex segments	
		No.	Percentage
Clupea harengus	1356	233	17·2
Clupea sprattus	129	23	17·8
Sardina pilchardus	115	15	13·0
Argentina silus	69	15	21·7
Gadus minutus	81	14	17·3
Gadus merlangus	107	37	34·6
Atherina presbyter	101	13	12·9

Kändler's data on flat-fishes show that in the plaice, flounder, dab and turbot, backbones with accessory spines on the penultimate vertebra may account for as much as from 30 to 40 % of a sample, while for diallel crossings of trout, Schmidt (1921) found that the 5th vertebra from the end of the column showed duplication of spines in about 10 % of his material. When it is remembered that these percentages, like those for the Plymouth material, do not include vertebral fusions and accessory processes in other parts of the backbone, it will be realized that the adjective "abnormal" is hardly applicable to the complex segments in the species named.

How is the peculiar nature and position of these segments to be accounted for, and how ought they to be counted in arriving at the number of vertebrae (*n*)? It is more convenient to consider the second part of this question first. Schmidt, Kändler and Ford are in agreement in finding that if a complex segment is counted as 1, the number of vertebrae (*n*) works out on average lower than the value of (*n*) for specimens in which complex segments do not occur. More striking, however, is the fact that in the trout, herring and plaice, this discrepancy between the corresponding averages approximates very closely to 0·5 vertebra. That is to say, if a complex segment be counted as $1\frac{1}{2}$ instead of 1, the average value of (*n*) is brought into agreement with the "normal" average. Whether this applies generally to all species in which complex vertebrae occur cannot at present be decided owing to lack of sufficient data. The following data for *Clupea sprattus*, *Sardina pilchardus*, *Argentina silus*, *Gadus minutus* and *G. merlangus*, are of some interest in this connexion, however:

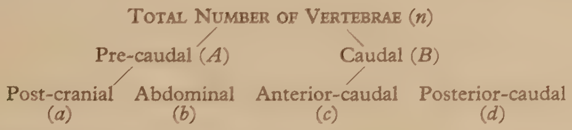
Species	No. of skeletons: Normal	No. of skeletons: Abnormal	Difference in average no. of vertebral segments counting each segment as 1
Clupea sprattus	102	23	0·59
Sardina pilchardus	100	15	0·37
Argentina silus	51	15	0·77
Gadus minutus	66	14	0·75
Gadus merlangus	63	37	0·67

Schmidt's hypothesis to account for his results is very interesting (Schmidt, 1921, p. 4). He suggests that vertebrate animals can realize fractional parts of vertebrae, but that such individuals are numerically inferior to what are ordinarily termed "normal" individuals. In reality, individuals with complex segments are just as "normal" as the latter. In both cases it is the individual's genetic structure in connexion with its environment in the sensitive period which is deciding the total realized; but it seems as if whole numbers in such organs as vertebrae are more easily realized than fractional parts.

This does not explain, however, why complex segments should occur only at fixed points in the vertebral series, usually at the caudal end. And it is difficult to see why the capacity to realize "fractional parts" of a vertebra should thus be confined to a given few among the many vertebrae of which the backbone consists. Consideration of this question brings to mind the theory of Kyle (1926, p. 82) that the number of vertebrae is determined under the combined influences of prevailing environmental conditions and the movements of the developing fish. Were this so, there is, perhaps, some possibility that vertebral variation might be more pronounced at the two ends of the vertebral column than elsewhere. In the absence of any new data which could throw further light on these fundamental matters, there is little purpose in continuing the discussion. In the meantime it is necessary to bear in mind that, in determining the number of vertebrae (n) in a sample of fish, care must be exercised in allowing for possible variation due to the presence of complex segments and other abnormalities in individual fish.

The Number of Vertebrae expressed as $n=(a+b+c+\dots)$

Seeing that (n) is by definition an integer, it can be expressed as the sum of other integers. With such obvious and sharp changes in the form of the vertebrae at definite points along the column, it is thus possible in practice to record (n) as the summation of successive groups of vertebrae. The vertebral column of a gadoid, for example, can first be divided into a pre-caudal group (A) followed by a caudal group (B). Group (A) can be sub-divided into an anterior post-cranial group (a) and a posterior abdominal group (b). Similarly, group (B) can be subdivided into an anterior-caudal group (c) and a posterior-caudal group (d). Expressed in diagrammatic form, the vertebral series is thus composed as follows:



Expressed mathematically, $n=(A+B)=(a+b+c+d)$.

Subdivision of the backbone into groups of vertebrae is normally possible in practically all species, but, as has already been pointed out in an earlier paragraph, certain individuals in almost every species will present difficulty on account of homoeotic variation at the junctions of the groups into which the vertebrae of the backbone are divided. To give an illustration in point, gadoid backbones will certainly occur in which there is a "transitional" form of vertebra between the typical pre-caudals and the typical caudals. There appears to be no reliable criterion upon which to judge whether this transitional vertebra ought to be counted as a pre-caudal vertebra or a caudal. In biometric investigations, where conclusions are to be drawn from a statistical treatment of vertebral counts, it would seem necessary, either to put backbones of this type in a class apart from "normal" backbones, or to make an arbitrary count of the transitional vertebra as (say) $\frac{1}{2}$ pre-caudal and $\frac{1}{2}$ caudal, thereby preserving the integer value of (n). For example, an abnormally constructed backbone of a whiting might thus be recorded either as $(n)=(A)+(1)+(B)$ or as $(n)=(A+\frac{1}{2})+(\frac{1}{2}+B)$. Further consideration of homoeotic variation will be found in p. 28.

The summation of (n) as $(a+b+c+\dots)$ is of practical utility in the study of variation from species to species. Again borrowing an illustration from the gadoid fishes, it is interesting to note that, within the genus *Gadus*, the difference in the value of (*n*) between species is, in the main, little more than a difference in the number of abdominal vertebrae (*b*). This is shown by a comparison of data for *G. merlangus* and *G. minutus*:

	Gadus merlangus	*Gadus minutus*	Differences
No. of individuals	63	66	—
Mean value of (*n*)	54·5	49·3	5·2
Mean no. of post-cranials (*a*)	4·0	4·0	nil
Mean no. of abdominals (*b*)	15·7	10·9	4·8
Mean no. of caudals ($c+d$)	34·8	34·4	0·4

The data show that of the total difference of 5·2 between the two mean values of (*n*), no less than 4·8 is accounted for by difference in the mean number of abdominal vertebrae (*b*), while the small remainder of 0·4 is distributed among the much larger number of caudal vertebrae.

In contrast with species of the genus *Gadus*, species of flat-fish (Order Heterosomata) tend to agree in the number of abdominal vertebrae but differ in the number of caudals. Thus, whereas the lemon sole (*Pleuronectes microcephalus*) and witch (*P. cynoglossus*) commonly have twelve pre-caudals, the number of caudals is about thirty-five in the lemon sole but forty-six in the witch. In the four local species of *Solea*, the number of pre-caudals is nine or ten, whereas the number of caudals varies from thirty to forty according to species.

The subdivision of (*n*) into group integers is also helpful in the study of the variation of (*n*) among individuals of the same species. In the herring, for example, it is well known that there is considerable individual variation in (*n*). In an earlier paper (Ford, 1933) the author has shown that individuals with a larger number of vertebrae (*n*) tend to have, on average, a disproportionately larger number of vertebrae in the well-differentiated “tail” group at the posterior end of the backbone. A similar study of 102 specimens of the sprat (*Clupea sprattus*) gives a corresponding indication, although, of course, the total number of specimens examined is hardly large enough to give conclusive results:

Total no. of vertebrae between skull and urostyle	Total no. of individuals	No. of vertebrae in “tail” group			“Tail” averages
		5	6	7	
46	28	9	18	1	5·71
47	70	7	59	4	5·96
				Difference	0·25

The increase of one vertebra from a total (*n*) of forty-six to a total of forty-seven thus results in an average increase of 0·25 in the number in the “tail” group. This is a disproportionately large increase, because if the difference of 1·0 between the values of (*n*) had been evenly distributed along the whole backbone, the increase in "tail" vertebrae would have been $\frac{1}{46} \times 5{\cdot}71 \doteq 0{\cdot}124$, instead of 0·25. Putting the facts in an alternative way, sprats with forty-six vertebrae have a "tail" group comprising $\frac{5{\cdot}71}{46} = 0{\cdot}124$ of the total (*n*), whereas sprats with forty-seven vertebrae have a "tail" group comprising $\frac{5{\cdot}96}{47} = 0{\cdot}127$ of the total (*n*).

It will be agreed that studies of this kind must have an important bearing upon the interpretation of observed differences in (*n*) during investigation of local populations of fishes. Where fish like herring, cod and plaice vary in the average value of (*n*) from place to place and from season to season, any information concerning the manner in which the differences in (*n*) are distributed along the length of the backbone may well prove of great significance and assistance in determining relationships between the different populations represented.

The Number of Vertebrae (n) as the Summation of a Linear Series

When considering the number of vertebrae simply and solely as an integer (*n*), no account is taken of the individuality of the vertebrae counted. A first step towards recognition of this individuality is taken when (*n*) is expressed as the sum of several groups of vertebrae, but ultimately it becomes necessary to regard (*n*) as the sum of a linear series of vertebrae, (*n*) in number. This series may be expressed as $(n) = (1\text{st} + 2\text{nd} + 3\text{rd} + \ldots + n\text{th})$. In the last analysis the absolute numerical value of (*n*) has lost none of its own significance, nor is the significance of (*n*) expressed as $(a + b + c + \ldots)$ in any way impaired; but, for the first time, due regard is paid to the anatomical character and ordinal position in the vertebral series of each and every segment included in the count. In many species it may be necessary to do this before it becomes possible to detect the ways in which vertebral variation is being expressed. Close attention may also have to be given to differences in vertebral form which are structural rather than numerical or geometrical, differences which must be described and figured rather than counted. The results, however, are no less important or valuable because they cannot be expressed in concise mathematical terms.

The Degree of Constancy in the Number of Vertebrae

It may seem almost a truism to observe that data on the degree of constancy in the number of vertebrae can only be acquired by the routine examination of individual after individual. The fullness of the information thus derived is dependent upon (*a*) the number of observations made upon each individual, and (*b*) the number of individuals examined. With regard to (*a*), it will be realized from what has been said in foregoing sections that the extent to which the simple integer (*n*) varies from individual to individual is only a part of the study of the degree of constancy in the number of vertebrae. Important though knowledge of variation in (n) *per se* may be and is, it requires to be supplemented by knowledge of variation from vertebra to vertebra along the length of the backbone. For experience shows that vertebral variation is not evenly distributed along the length of the vertebral column, but more pronounced in some parts than in others. Stability in the value of (n) for a species, therefore, does not imply the entire absence of vertebral variation throughout the length of the backbone, any more than variability in (n) implies that the whole of the backbone is unstable.

Concerning the number of individuals examined in a study of the degree of constancy in the number of vertebrae, it need hardly be said that every additional specimen examined provides entirely new and independent data. No statement on the degree of vertebral constancy is therefore complete unless it includes the number of individuals examined. Moreover, the greater the number of individuals examined, the greater the value of the results obtained. During the investigations at Plymouth, every endeavour has been made, as opportunity has allowed, to add to the number of individual backbones of each species studied. It is hoped that this practice may be continued until sufficient data have been accumulated to yield a reasonably reliable indication of the range of vertebral variation in each. In the present paper it is proposed to restrict attention to data on eight species which will serve to illustrate the nature of the observations being made in this study of constancy.

Clupea harengus.

It is convenient to commence with the herring, not only because some thousands of backbones of this species have been examined at Plymouth in connexion with the routine investigation of the herring fisheries there, but because the species, in common with its allies in the family Clupeidae, is characterized by widespread variation in vertebral form. The features of the clupeoid backbone and its variation are described on p. 36, and without doubt, a single sample of not more than 100 herrings will provide an investigator with ample evidence of this variation. Almost certainly, the following phenomena will be observable:

(1) Variation in the integer value of (n) amounting to from four to six vertebrae.

(2) Structural "abnormalities" in as many as 20 % of the specimens which affect the computation of (n). These are of the following kinds:

(*a*) Complete or incipient duplication in one or more segments (Text-fig. 8).

(*b*) Duplication of the neural or haemal spines (or both) on the two vertebrae immediately preceding the urostylar (terminal) segment (Text-fig. 10).

(3) Variation in the value of (n) written as $(a+b+c+\ldots)$ in accordance with structural change along the length of the column.

(4) Homoeotic variation at the junctions of adjacent groups of vertebrae into which the backbone is divisible. Included under this head are the many

cases of bilateral asymmetry which commonly occur, in which the characters of an anterior group are seen on the one side and those of a posterior group on the other. In a sample of 100 fish, as many as 80 may show such asymmetry in one or more of the following positions:

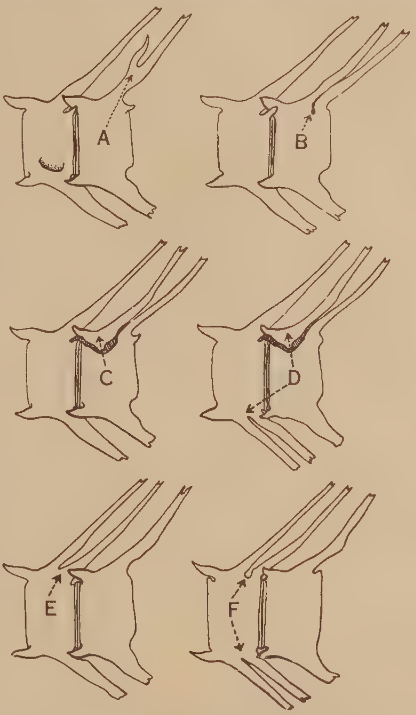
(*a*) In about the 24th vertebra, where the parapophyses cease to be rib-bearing and "autogenous" from the centrum, and become fused to the centrum (Text-fig. 11).

(*b*) In about the 27th vertebra, where the neural spines cease to be "autogenous" (Text-fig. 11).

(*c*) In about the 50th vertebra, at the anterior end of the "tail" group of vertebrae in which the haemal spines are cross-tied to the centra (Text-fig. 2 on p. 7).

(5) Abnormalities shown by the processes in isolated vertebrae along the length of the backbone (Text-fig. 8).

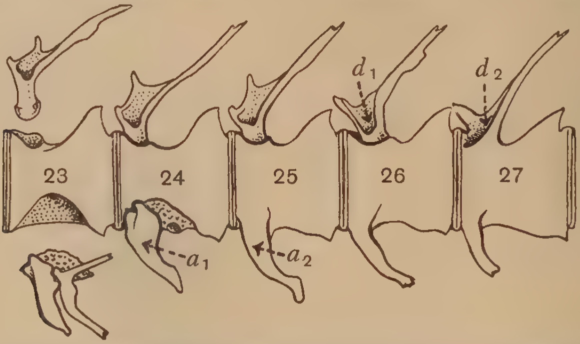
Actual data concerning variation of types 1, 2, 3 and 5 will be found in an earlier paper (Ford, 1933). It must here be said, however, that when these data were collected, bilateral asymmetry of types 4 (*a*), (*b*) and (*c*) was not noted. So far as my own data are concerned (Ford, 1933) it may be accepted that they are at least consistent in the one respect that they relate to counts made along the left side of the body—a consequence of an arbitrary practice in the routine adopted.



Text-fig. 10. Doubled-spined vertebrae at tail-end of herring. From Ford (1933). In each of the diagrams the two vertebrae represented are those immediately anterior to the complex terminal (urostylar) segment.

Scomber scombrus (Plate IX, fig. 1 and Text-fig. 4).

In contrast with the highly variable backbone of the herring, that of the mackerel (*Scomber scombrus*) is very stable. Data are available for a total of 1219 backbones examined at Plymouth by my colleague, Mr P. H. T. Hartley, in connexion with a programme of mackerel research now in progress at the Laboratory. Out of this total there were only eight in which the number of vertebrae (*n*) differed from thirty-one. Of the eight variates, five had thirty vertebrae and three had thirty-two. Of the remaining 1211, all save four further agreed in having thirteen pre-caudal vertebrae and eighteen caudals. This left 1207, of which 1201 still further agreed in having a well-defined "tail" group of six vertebrae (3+1+1+1) at the posterior end of the column (Text-fig. 4). That is to say, 98·5% of the original total of 1219 agreed in having the vertebral formula $(n)=31=(13+18)=13+(12+3+1+1+1)$. With an important exception, the comparison of backbones, vertebra by vertebra, throughout the length of the column, confirmed this high degree of vertebral stability in the mackerel. The 9th, 10th and 11th vertebrae, especially the 10th, were alone in exhibiting noticeable variation, consisting of individual differences in the extent to which definite haemal arches were developed. A total of 1207 specimens examined could thus be segregated in five groups as under:



Text-fig. 11. Autogenous neural and haemal processes in the herring. From Ford (1933). In the diagram, d_1 is the last of the autogenous neural spines, and a_1 the last of the autogenous haemal arches.

	Serial no. of vertebra			
Group	9th	10th	11th	No. of specimens
1	Closed haemal arch	Closed haemal arch	Closed haemal arch	1
2	Absent	Closed haemal arch	Closed haemal arch	530
3	Absent	Open haemal arch	Closed haemal arch	437
4	Absent	Absent	Closed haemal arch	230
5	Absent	Absent	Open haemal arch	9
				1207

These results may be summarized in the statement that the great bulk of mackerel examined at Plymouth only vary in the condition of the haemal arch on the 10th vertebra. Mr Hartley is at present investigating the possible utility of this variability in the study of the different populations of mackerel frequenting south-western waters.

Caranx trachurus (Plate IX, figs. 2 and 4 and Text-fig. 3).

The remaining six species to be considered are similar to the mackerel in showing a high degree of constancy in the total number of vertebrae (n), as well as in (n) expressed as $(a+b)$, where (a) is the number of pre-caudal vertebrae and (b) the number of caudals. The first of these is *C. trachurus*, of which the total number of specimens examined is 111. Of these, 110 had twenty-four vertebrae, comprising ten pre-caudals and fourteen caudals. The single exception had twenty-five vertebrae, the extra vertebra being in the caudal region as an interpolation behind the normal 22nd vertebra. Of the 110 specimens with twenty-four vertebrae, sixty-five agreed in having the formula

$$(n)=24=(10+14)=(1+7+2)+(1+4+4+2+1+1+1).$$

The characters upon which this formula is based are as follows:

Serial no. of vertebrae	Character
1	Neural spine "autogenous"
2–8	Open parapophyses
9–10	"Bridged" parapophyses
11	1st caudal vertebra; without ventral pre-zygapophyses
12–15	Ventral pre-zygapophyses well developed
16–19	Haemal arch foraminated
20–21	First two of "tail" group of vertebra; neural and haemal spines short and depressed along length of backbone
22	Epural very long; hypural "autogenous" from vertebral centrum
23	Neural arch reduced; hypural "autogenous" from centrum

Turning to the remaining forty-five specimens it was found that these showed variation from the characters enumerated above. The positions along the vertebral series at which this variation occurred, and its extent, are shown in the following summary:

Serial no. of vertebra	Nature of variation	No. of occurrences
8	Parapophyses "bridged" instead of being open	3
9	Parapophyses open instead of being "bridged"	3
11	Ventral pre-zygapophysis present on both sides	1
	Ventral pre-zygapophysis present on one side only	2
12	Ventral pre-zygapophysis present on one side only	4
14	Haemal arch of one side is foraminated	9
15	Haemal arch foraminated on both sides	4
	Haemal arch foraminated on one side only	14
16	Haemal arch of one side without foramen	13
	Haemal arch of both sides without foramen	6
17	Haemal arch of one side without foramen	2

It will be realized that all the above types of variation can be regarded as homoeotic. The abnormalities in the 8th, 11th, 14th and 15th vertebrae are cases of *backward* homoeosis (see Bateson, 1894, p. 111), in that these vertebrae show features which more properly belong to vertebrae which are farther back in the ordinal series. The abnormalities in the 9th, 12th, 16th and 17th, on the other hand, are examples of *forward* homoeosis, since the vertebrae concerned have a form approaching that of vertebrae which stand in front of them.

Summarizing the observations so far made on *Caranx*, it is seen that vertebral variation is chiefly confined to the haemal arches of the 14th, 15th and 16th vertebrae which may, or may not, be foraminated on both sides. Some variation may also occur in the 8th, 9th, 11th, 12th and 17th vertebrae, although less frequently.

Mullus surmuletus.

A total of 154 red mullet (*Mullus surmuletus*) has been examined without finding a single exception to the number of vertebrae (n) being twenty-four, comprising ten pre-caudals and fourteen caudals, as in *Caranx* and many other Perciform fishes. Such variation in vertebral form as occurred was localized in the 7th, 9th, 10th and 11th vertebrae, the remaining vertebrae appearing very stable. Dealing first with the 7th vertebra, it was found that in 105 specimens the parapophyses of this vertebra were open, whereas in the remaining forty-nine they were closed by bridging. The latter forty-nine may thus be considered cases of backward homoeosis, in which the 7th vertebra has assumed a character of the normal 8th. In the region of the 9th to 11th vertebrae, ventral pre-zygapophyses make their appearance. The following table shows the extent of variation in this respect:

	Serial no. of vertebra			No. of specimens
	9th	10th	11th	
Ventral pre-zygapophyses present or absent	Present on one side only	Present on both sides	Present on both sides	5
	Absent	Present on both sides	Present on both sides	56
	Absent	Present on one side only	Present on both sides	60
	Absent	Absent	Present on both sides	30
	Absent	Absent	Present on one side only	3

Subject to the above exceptions, therefore, the backbone of the red mullet will conform to the formula, $(n)=24=(10+14)=(1+6+3)+(11+1+1+1)$.

Morone labrax (Plate VII and Text-fig. 1).

The backbone of the bass (*M. labrax*) normally comprises twenty-five vertebrae, expressible as $(12+1+12)$, as shown in Plate VII, fig. 1. Out of 107 specimens so far examined, there were only two exceptions to this. The exceptions were particularly interesting in that both exhibited duplication of the neural spines of the 1st vertebra. If, on this account, the 1st vertebra is counted as two instead of one, the total number of vertebrae (n) is restored to the normal $(12+1+12)$. The determination of the number and ordinal position of the vertebrae with closed haemal arches showed that in ninety-three of the total of 107 specimens the haemal arches of the 10th, 11th and 12th vertebrae were closed. In eight of the remaining specimens the arches of the 9th vertebra were also closed, while in the six others, only the 11th and 12th had closed arches. Elsewhere along the backbone there was no very noticeable variation, and the "type" for the species could thus be expressed as

$$(n)=25=(12+1+12)=(1+8+3)+1+(9+1+1+1).$$

Scorpaena dactyloptera (Plate XII, fig. 2).

Seventy-five out of seventy-seven specimens of this species examined agreed in having twenty-five vertebrae, and in the following table the extent of further agreement, vertebra compared with vertebra along the ordinal series, is summarized:

Scorpaena dactyloptera. *Variation among individuals with twenty-five vertebrae*

Serial no. of vertebrae	Characteristics	No. of normal individuals	Variates	
1	Neural arch autogenous	75	—	
2	Neural spine of same height as, and applied to, neural spine of 1st vertebra. No parapophyses	75	—	
3–4	Have tallest neural spines, parapophyses absent	75	—	
5	No parapophyses	75	—	
6	With short, unbridged parapophyses	75	—	
7–10	Haemal arches bridged and foraminated	75	—	
11	Similar to 10th	72	Foramen on one side only ...	3
12	Similar to 10th	40	Foramen on one side ... ... Foramina absent	20 15
13–17	Haemal arches not foraminated	73	Foramina on 13th ... ... Foramina on 14th	1 1
18	Similar to 17th	71	Foramina on 18th	4
19	Similar to 17th	67	Foramina on 19th	8
20	Haemal arches foraminated	59	Foramen on one side only ... Foramina absent	13 3
21–22	Similar to 20th	75	—	
23	Epural elongate, hypural autogenous	75	—	
24	Neural arch reduced, hypural autogenous	75	—	
25	Anterior hypural "hooked"	75	—	

It is seen from the above data that vertebrae 1–10, and 21–25, are very stable in form. Such variation as occurs in vertebrae 11–20 consists of bilateral asymmetry in respect of the fenestration of the haemal arches, and may be regarded as homoeotic in nature. The "type" form of backbone in this species may be written as $(n)=25=(1+1+3+1+6+7+3+1+1+1)$.

Mugil spp. (Plate XI).

Of the grey mullets (*Mugil*) which occur at Plymouth, one is the thick-lipped grey mullet (*M. chelo*), of which 116 specimens have so far been available for study. All except four of these have twenty-four vertebrae made up of $(11+13)$. Of the four exceptions, three have twenty-five vertebrae $(11+14)$, leaving one with twenty-three vertebrae $(11+12)$. The most frequently occurring form of backbone has the formula

$$(n)=24=(11+13)=(1+1+5)+1+3+(1+10+1+1).$$

As to variations from it, there are six backbones which show a weak transverse bridge across the parapophyses of the 11th vertebra, whereas normally the parapophyses are open. The 8th vertebra, also, is subject to variation in that it sometimes bears a ventral post-zygapophysis on one or both sides of the centrum, whereas normally this zygapophysis is first seen on the 9th vertebra.

Thin-lipped grey mullets also occur at Plymouth which, failing specific identification, have been recorded as *Mugil* spp. The backbone of this form is at once distinguished from that of the thick-lipped *M. chelo* by the reticulated surface of the centrum throughout the vertebral column. Only thirty-four specimens have at present been available for study, but of these, thirty-two agree with *M. chelo* in having twenty-four vertebrae, made up of $(11+13)$. The remaining two have $25=(11+14)$ and $23=(11+12)$, respectively. The normal specimens also agree with *M. chelo* in having laminated neural spines to the first seven vertebrae, and open parapophyses on vertebrae 1–11. No case of bridging across the parapophyses of the 11th vertebra was observed (cf. *M. chelo*). There is a difference from *M. chelo* in that the ventral post-zygapophyses usually appear for the first time on the 8th vertebra instead of on the 9th. The typical thin-lipped grey mullet thus has the formula

$$(n)=24=(11+13)=(1+1+5)+4+(1+10+1+1).$$

Reviewing the observations given above, the important point emerges that each species examined presents one or more centres of definable variation along the length of the vertebral column, even though the total number of vertebrae and other major vertebral counts remain for all practical purposes constant. Furthermore, the data given are sufficient to indicate the number of individual backbones of any one species which must be examined in order to arrive at a fair estimate of the nature, ordinal position and extent of such variation. Information of this kind is clearly of practical help to an investigator intending to utilize vertebral data in the course of population or "race" studies of fish, since it shows which characters are likely to prove of the greatest service. It matters little to him that vertebral variation in some species is seen only in structures of comparatively minor anatomical or physiological significance. The all-important fact for his purpose is that there is actual variation which can be evaluated with mathematical precision, whether that variation be in the backbone as a whole or confined to one small part of it. For example, in an enquiry into the possibility of different populations of mackerel occurring in south-western waters, it may prove of great assistance to know that individual mackerel differ from one another in the condition of the haemal arch on the 9th to the 11th vertebrae, whereas in other respects the vertebral column is very stable. The collection and comparison of data on this variable character in samples of mackerel from different parts of the area, or at different times, may reveal population differences of considerable local significance—a finding which will be in no way affected by the circumstance that the actual vertebral difference itself is of no very great importance anatomically.

The above study of the degree of constancy in vertebral character also demonstrates the fact that no species has a backbone which is rigidly constant in form from individual to individual. Provided that the backbone is studied in sufficient detail, variation of some kind will become evident. The nature and extent of that variation varies from species to species and according to the genus, family and order to which the species is referable.

The Vertebral Column in Taxonomy and Phylogeny

In coming to consider the backbone as an indicator of identity and natural affinity, it is necessary to bear in mind certain facts. In the first place, the material available for study is here limited largely to species of a local fauna. Due caution must therefore be exercised in drawing generalized conclusions from the observations made. Secondly, the value of a vertebral character, either as a clue to identity or as an indicator of affinity, is of a *relative* rather than an *absolute* nature, since it varies according to the circumstances in which it is evaluated. There are times when a given character will establish identity or indicate affinity when other characters fail to do so, but there are other times when it is barely worth considering. The third point to be noted arises out of the second. For if a vertebral character is to be of any use at all in taxonomy or phylogeny, it must present a reasonable degree of constancy from individual to individual within the species to which it relates. One further fact requires to be mentioned, namely, that in taxonomy and phylogeny no feature of the vertebral column is too insignificant to be worthy of attention. A character may be insignificant in an anatomical or physiological sense, and yet be far from trivial in its taxonomic and phylogenetic import.

Since the work at Plymouth first began, backbones belonging to fishes of thirteen orders of the subclass Neopterygii have been examined. It is hoped that it may be found possible in due course to publish descriptive accounts of these, order by order, but in this first paper it has been thought more desirable to take a brief survey of the material as a whole, with the idea of showing by what means and with what measure of success it is possible to establish identity and natural relationship within the orders of fishes represented.

Order Isospondyli

The following species of this order have been examined:

Family	Genus	Species
Clupeidae	*Clupea*	*harengus, sprattus*
	Alosa	*alosa, finta*
	Sardina	*pilchardus*
	Engraulis	*encrasicholus*
Salmonidae	*Salmo*	*salar, trutta*
Argentinidae	*Argentina*	*silus*

As already indicated when considering the vertebral variation of the herring (p. 28), the fishes of this order are characterized by great plasticity in vertebral form. Indeed this excessive plasticity might almost be considered one of the distinguishing vertebral characters of the order. Even so, it is easy to see in the backbone ample evidence of similarity in basic form among the different species. Perhaps the first character which should be mentioned is the presence in every species of "autogenous" neural or haemal (or both) processes on an appreciable number of the vertebrae. The disposition of these in different genera is shown in the following table:

Autogenous neural processes	Autogenous haemal processes	Genus
On anterior pre-caudal vertebrae, and on hindermost "tail" vertebrae	On anterior pre-caudal vertebrae, and on hindermost "tail" vertebrae	*Salmo*
On anterior pre-caudal vertebrae only	On anterior pre-caudal vertebrae, and on hindermost "tail" vertebrae, as in *Salmo*	*Argentina*
On anterior pre-caudal vertebrae only	On anterior pre-caudal vertebrae only	*Clupea*, *Alosa*, *Sardina*
On anterior pre-caudal vertebrae, except vertebrae 1 to 3–4	None	*Engraulis*

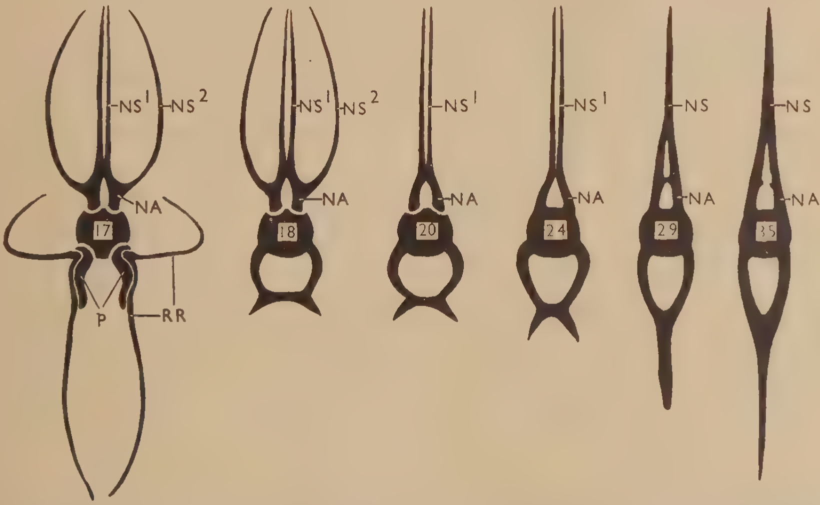
It is seen that this one character is sufficient to segregate the fishes according to Regan's classification. The presence of autogenous processes in the "tail" vertebrae of *Salmo* and *Argentina*, but not in those of the Clupeidae, is thus in keeping with Regan's classification of the Salmonidae and Argentinidae in a suborder (Salmonoidea) apart from the Clupeidae (suborder Clupeoidea).

The species of the family Clupeidae have backbones full of interest in their agreements and disagreements. In considering these it will be of much assistance to deal first with the characters of the skeleton of a shad (*Alosa alosa*), measuring approximately 26 in. in length which I was fortunate enough to secure at Plymouth in May 1937. The comparatively large size of the bony structures in this specimen makes it the more easy to see the points of interest. It is built up of fifty-seven vertebral segments, each of which has its own form, dependent upon the precise position it occupies in the vertebral series. In no other backbone is the fact more clearly shown that each vertebra is a set-piece in the composite and graded pattern of the backbone as a whole. Every part and process of each vertebra indicates by its form the one and only position in the backbone into which it will fit. The composite nature of the vertebral pattern is shown by an abrupt change in vertebral form at certain points along the column. At least six such changes in form are worthy of note, whereby the backbone may be divided into distinct regions along its length. The following description of these changes will be easier to follow by the aid of the illustrations in Plate I and Text-fig. 12.

Vertebrae 1 *and* 2. These two vertebrae are clearly modified to form a union between the backbone and the skull.

Vertebrae 3–17. In this region the neural and haemal processes of all the vertebrae are autogenous from the centrum. Dorsally, the neural spines of the right and left side are bifurcate structures (Text-fig. 12) which stand by their peg-like bases in sockets in the centrum (Plate I). Above the spinal cord the inner elements of the bifurcate spines of the two sides are brought into adjacency in the middle line, but they do not fuse together to form a single composite neural spine. Ventrally, the rib-bearing haemal arches are also autogenous from the centra, and can be easily dissected away in their entirety from the latter (Plate I).

Vertebrae 18–23. In the 18th vertebra an abrupt change occurs in the condition of the haemal arches. These no longer bear ribs, become continuous with the centra, and are transversely bridged to enclose a haemal canal (Plate I). At the same time the form of the ventral post-zygapophysis is showing signs of a change from the more simple thorn-like form of the anterior vertebrae to the irregularly reticulate form characteristic of this region. Meanwhile along the dorsal surface, the neural spines remain autogenous, although from the 20th vertebrae onwards they no longer possess the second spiny element shown by the vertebrae in front (Text-fig. 12).



Text-fig. 12. *Alosa alosa*. To show the changes in form along the backbone. The serial numbers of the vertebrae are inserted on the ends of the centra. Where processes are autogenous they are broken from the centrum by a white line. *NA*, neural arch; *NS* neural spine; *P*, parapophysis; *RR*, ribs.

Vertebrae 24–28. In the 24th vertebra the neural spines for the first time cease to be autogenous and become continuous with the centrum at their bases (Plate I). As in the anterior vertebrae, however, the right and left halves still retain their separate identity throughout their length (Text-fig. 12). Ventrally, the distal forked ends of the haemal arches outside the haemal canal are beginning to elongate and close together. On the right side of vertebra 24 and on the left of vertebra 25, there appears for the first time a slender but elongate pre-zygapophyseal process at the base of the haemal arch (Plate I). This process becomes progressively more robust in later vertebrae, taking up a position parallel to the length of the column.

Vertebrae 29–49. In the 29th vertebra another change occurs in the condition of the neural arch. It now shows two separate canals, the lower one to house the spinal cord, and the upper one to carry the dorsal ligament. Above these canals the hitherto discrete right and left neural spines have become fused together to form a single, composite neural spine (Text-fig. 12). In vertebra 34 the transverse division between the neural canal and ligament canal breaks down, and both spinal cord and ligament appear then to be housed within a single neural canal. Ventrally, the distal ends of the haemal spines have at last come completely together, rapidly lengthening from vertebrae 29 to 34. In this comparatively long section of the column, too, it is easy to see the gradational change in form of the zygapophyseal processes, particularly the dorsal and ventral pre-zygapophyses, which assume greater and greater dominance as one passes towards the posterior end of the backbone.

Vertebrae 50–57. The 50th vertebra is the first of the terminal "tail" section comprising eight vertebral segments. It differs from the 49th in that the base of the haemal spine on either side is cross-tied to the centrum by a bony bar which is not present in earlier vertebrae. In *Alosa* this cross-tying is not so easily visible as in the herring but it is nevertheless present. In other respects the vertebrae in this section are much more rigidly locked together than those in front, a condition undoubtedly associated with the function of this part of the backbone as a skeletal framework and support for the caudal fin.

With this description of *Alosa* available it is easier to turn to a comparison with the other species of the Clupeidae, for these are manifestly built along the same general lines. That is to say, while the total number of vertebrae, the number of vertebrae in corresponding regions, and the more minute structure of corresponding skeletal structures, will all vary from species to species, the same basic plan and pattern is evident in them all. *Engraulis encrasicholus* is perhaps the most divergent in that none of the haemal arches of the pre-caudal vertebrae is autogenous from the centrum, or transversely bridged to form closed haemal arches as in *Alosa* and the others. Despite this there remains abundant evidence of the clupeoid basic plan in the other vertebral characters. The backbone of *Sardina pilchardus*, on the other hand, resembles that of *Alosa* to a decided degree. Those of the two species of *Clupea* (*C. harengus* and *C. sprattus*) go well together save in the total number of vertebrae, and agree in being constructed on a more simple and generalized note than either *Alosa* or *Sardina*.

It remains to be said in this general survey that there is a very considerable degree of variation among individuals in each of the species examined. While this in no way masks either the similarities or distinctions between species, it does make it of great importance in biometric studies of local populations to exercise caution in interpreting the significance of observed differences in vertebral form. In other words, one needs to be conversant with the manifold ways in which the vertebrae of a clupeoid backbone may vary, if one wishes to utilize vertebral data in such researches.

Order Anacanthini

All save one of the fishes of this order which have been examined belong to the family Gadidae, the single exception being *Merluccius merluccius*, of the family Merlucciidae:

Family	Genus	Species
Merlucciidae	*Merluccius*	*merluccius*
Gadidae	*Gadus*	*callarias, aeglifinus, luscus, minutus, merlangus, poutassou, virens, pollachius*
	Urophycis	*blennoides*
	Molva	*molva, byrkelange, elongata*
	Mora	*mediterranea*
	Onos	*mustelus, cimbrius* (also two species of three-bearded rockling)
	Raniceps	*raninus*
	Brosme	*brosme*

The condition of the vertebral column in these gadoid fishes (Plates II–VI) shows how each species is really a unique modification of a single "gadoid type" of backbone. In each of them, including *Merluccius*, the backbone is divisible into four sections, (*a*) post-cranial, (*b*) abdominal, (*c*) anterior caudal, and (*d*) posterior caudal. Within each section, all species agree in the following ways:

In the post-cranial section:

The dorsal post-zygapophyses on the first two or more vertebrae are laterally placed and backwardly directed.

The 1st neural spine is in close association and of the same height as the supra-occipital.

In the abdominal section:

The well-developed parapophyses are all open.

The neural spines of the most anterior of the vertebrae are lancet-shaped.

There are open grooves in the neural arches (in contrast to foramina) for the passage of the spinal nerves. (*Onos* spp. in part are an exception.)

In the anterior caudal section:

The closed haemal arches of the most anterior vertebrae form a "haemal funnel".

Open nerve grooves are present in the neural arches, as in the abdominal section (see above).

The distal ends of the neural spines are attenuated.

In the posterior caudal section:

The neural spines support the rays of the caudal fin.

The penultimate vertebra lacks neural spines, and its hypurals are autogenous.
The terminal segment is of characteristic form.

Although there is this measure of general agreement among the species, each has its own distinctive form. The difference between species lies both in the number of vertebrae in the successive sections of the backbone and in the form of the actual vertebral structures. Detailed descriptions would be out of place in this summary, but it may be helpful to give a list of characters which have been found serviceable in identification:

In the post-cranial section:
- Departure from the normal "neck" of four vertebrae (3 + 1).
- The form of the 1st vertebra and its neural arch and spine.
- The relative heights of the first three neural spines.

In the abdominal section:
- The number of vertebrae.
- The degree of elaboration of the parapophyses.
- The presence or absence of apophyses in addition to parapophyses.
- The shape of cross-sections of the vertebral centra.

In the anterior caudal section:
- The number of vertebrae.
- The degree to which the "haemal funnel" is developed.

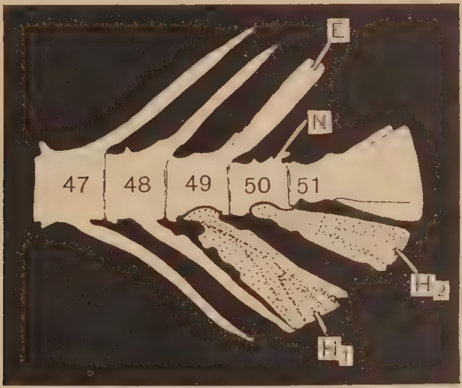
In the posterior caudal section:
- The number of vertebrae.
- The overall shape enclosed between the distal ends of the neural and haemal spines (e.g. whether compressed or attenuated).
- Whether or not the hypural of the antepenultimate vertebra is autogenous.
- The occurrence of duplicate neural and haemal spines on the antepenultimate vertebra.

In the backbone as a whole:
- The number of vertebrae $(n) = (a + b + c + d)$, and its degree of variation from individual to individual.
- The varying length of the vertebral centra along the column.
- The extent of the sculpturing of the vertebral centra.

Knowledge of these and other vertebral characters not only enables an observer to identify the species but to segregate species on the evidence of similarities in vertebral form. Thus, within the genus *Gadus*, five such groups can be made, viz.

(1) *G. aeglifinus*
(2) *G. poutassou*
(3) {*G. callarias*, *G. merlangus*}
(4) {*G. luscus*, *G. minutus*}
(5) {*G. pollachius*, *G. virens*}

Reference has already been made on p. 11 to the recognition of two forms of three-bearded rockling (*Onos* spp.) in the Plymouth fauna, differing in backbone characters. Another observation which may be referred to here has also been indicated on an earlier page (p. 7), namely, that in *Merluccius*, *Raniceps* and *Urophycis*, the form of the last three vertebrae recalls to a very appreciable extent the form of the similar section of the backbone in the more generalized percoids (Text-fig. 13). Whether or not this may be used as evidence of phylogenetic relationship is a matter which cannot be pursued here. It is to be noted that there is a further point of agreement with the generalized percoids in that *Merluccius*, *Raniceps* and *Urophycis* have eggs with oil globules. Here again, although no further discussion of the implied significance in phylogeny of the presence of an oil globule in the teleostean eggs is proposed, the point is one which might bear further examination, as it will again come to notice when dealing later with other orders of fishes.



Text-fig. 13. Tail-end of hake (*Merluccius merluccius*), showing the autogenous hypurals H_1 and H_2, the elongate epural *E*, and the crested neural arch *N*. Compare with the generalized tail vertebrae of the Perciform fishes, e.g. *Morone labrax* in Text-fig. 1.

Order Percomorphi

In contrast with the Anacanthini, the fishes of the order Percomorphi which have been examined represent no less than five suborders, seven divisions of these suborders, and sixteen families.

Suborder	Division	Family
Percoidea	Perciformes	Serranidae, Carangidae, Mullidae, Sparidae, Cepolidae
	Labriformes	Labridae
	Trachiniformes	Trachinidae
	Ammodytiformes	Ammodytidae
	Callionymiformes	Callionymidae
Scombroidea	—	Scombridae
Blennioidea	Blenniiformes	Blenniidae, Anarhichadidae
	Cliniformes	Pholidae
Gobioidea	—	Gobiidae
Mugiloidea	—	Mugilidae, Atherinidae

In view of this diversity of material it is not altogether surprising to find that it is practically impossible to discover vertebral characters applicable to the whole order. This does not mean that the backbone fails to show underlying relationship between fishes of the different genera and families. Quite on the contrary, the phylogenetic indications, given by the vertebral characters, of specific variation from a distinct percoid "type" are numerous and plain. This percoid "type" is best seen in species of the division Perciformes, sub-order Percoidea, of which *Serranus cabrilla*, *Caranx trachurus*, *Mullus surmuletus*, *Pagellus centrodontus*, *Cantharus lineatus* and *Box boops* have been studied at Plymouth. In these the backbone shows the following characters:

(1) The total number of vertebrae (n) is $24=(10+14)$ and is remarkably constant.

(2) The neural arch of the 1st vertebra is autogenous from the centrum (Plate IX, fig. 4).

(3) A certain number of the posterior parapophyses are closed by bridging to form a haemal canal.

(4) The last three vertebral segments have the following characters (Text-fig. 1):

- (*a*) Antepenultimate vertebra.
  Hypurals autogenous from centrum, and epurals elongated.
- (*b*) Penultimate vertebra.
  Hypurals autogenous from centrum, neural arch low and crested but without prominent neural spine.
- (*c*) Terminal vertebral segment.
  The foremost hypural is autogenous and bears a characteristic "hook".

The extent to which other species of Percomorphi agree with or differ from the most generalized Perciformes in the form of the backbone is most conveniently discussed, character by character.

(1) *The Number of Vertebrae*

It can hardly be doubted that within the order Percomorphi the number of vertebrae is very stable for many species, and it must be considered more than coincidence that so many of the most generalized species agree in having $(n)=24=(10+14)$. Yet, as has been shown at an earlier stage, (n) may be different from 24 without any loss of constancy. Thus it is 25 in *Morone labrax* and 31 in *Scomber scombrus* with quite remarkable regularity. On the other hand, there are many species of Percomorphi in which (n) is not only different from 24, but is subject to individual variation, sometimes appreciable. In *Cepola rubescens*, for example, in the small total of twenty specimens examined there were seven which showed either fusion of adjacent vertebrae at some point along the vertebral column or duplication of the neural or haemal spines on the penultimate vertebra, while (*n*) in the remaining thirteen specimens varied from 69 to 72. In *Atherina presbyter*, out of a total of 101 specimens there were twenty-six which showed either fusion of adjacent vertebrae or duplication of neural or haemal spines, while among the remainder (*n*) varied from 49 to 52.

(2) *The Autogenous Neural Spine of the 1st Vertebra*

This feature has been observed over a wide range of species. All the eight species of Perciformes examined show it, including *Cepola rubescens*. In the Labriformes it is present in the five wrasses, *Labrus bergylta*, *L. mixtus*, *Crenilabrus melops*, *Ctenolabrus rupestris*, and *Centrolabrus exoletus*. It is also present in *Trachinus vipera*, and *T. draco* which belong to the Trachiniformes. It is not seen, however, in *Ammodytes* and *Callionymus*. In the Scombroidea the 1st neural spine is fused to the centrum in *Scomber*, but (as shown by Kishinouye, 1923) it is detachable from the centrum in some species of the family Cybiidae. Even in *Katsuwonus* it is but feebly attached. In the Blennioidea, the spine is again autogenous in *Anarhichas* and *Pholis*, but not in *Blennius*. It is not autogenous in either *Mugil* or *Atherina*.

(3) *The Condition of the Parapophyses*

The closing of the haemal arches of two or more of the posterior caudal vertebrae by bony bridges is a character shared by the Plymouth Perciformes with the exception of *Cepola*, although there is variation from species to species in the number of these bridged parapophyses. In *Caranx trachurus* only the 9th and 10th vertebrae normally show them, whereas in other species they may be present on the 7th and 8th as well. Among the Labriformes the bridging tends to be masked by the increased length and lateral spread of the distal ends of the parapophyses, giving the appearance of "open" parapophyses. Actually, bridges are normally present in *Labrus bergylta*, *Crenilabrus melops* and *Ctenolabrus rupestris*, but not in *Labrus mixtus*. Of the two specimens of *Centrolabrus exoletus* examined, one shows no bridging, and the other incomplete bridging on the two hindermost pre-caudals. Closed parapophyses are also present in *Trachinus* and *Ammodytes*. In *Scomber* it is only on the 10th–13th vertebrae that parapophyses occur at all and these are closed. Among the Blennioidea, bridged parapophyses are seen in *Blennius*, but in *Anarhichas* they are all open; in *Pholis* there is an unusual condition of closed haemal arches in a long series from the 4th vertebra backwards. Those of the 4th and 5th vertebrae are connected at their distal ends by a longitudinal keel. In the gobies, bridging of the wrasse type is seen, but in both *Mugil* and *Atherina* the parapophyses are open.

(4) *The Condition of the "Tail" Section*

The type of "tail" section described in characters 4 (*a*), (*b*) and (*c*) above is met with in numerous species. As might be expected it is particularly common among fishes of the division Perciformes. A brief survey of the skeletons in the British Museum (Natural History), South Kensington, showed that it is present in species of the following families:

Serranidae, Kuhlidae, Centrarchidae, Chilodipteridae, Percidae, Pomatomidae, Carangidae, Menidae, Centropomidae, Arripidae, Lutianidae, Sciaenidae, Mullidae, Scorpaenidae and Scorpididae.

It is not suggested that all the species of all the families named will be found to agree in this character, or that it does not also occur in species of families not included in the list. The latter is merely given as a guide to the wide range of perciform fishes in which the generalized form of "tail" section has been observed. It may be added, however, that in ten species of the family Cichlidae there was an important variation, in which the hypurals of the antepenultimate vertebra were no longer autogenous from the centrum.

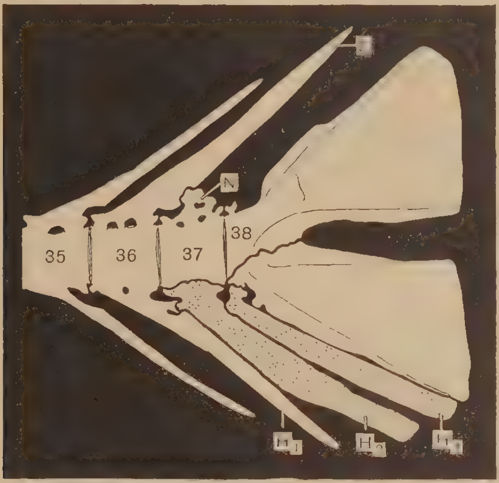
Outside the Perciformes, the form of the "tail" section tends to show departure from the generalized form, although it is fully retained in *Scomber scombrus* (Text-fig. 4, p. 8). Here, despite the distinctive modification of the caudal peduncle which characterizes the mackerel, the characters 4 (*a*) and (*b*) are clearly visible, while the well-developed hook on either side of the middle line of the terminal segment at once recalls character 4 (*c*). This basic similarity between the tail skeleton of the highly specialized mackerel and that of the generalized perciform is surely of particular interest.

In the Labriformes (Text-fig. 14) and Trachiniformes the "tail" section shows a slight deviation in character 4 (*a*), in that although the epurals of the antepenultimate vertebra are elongate, the hypurals are now continuous with the centrum instead of being autogenous. In the penultimate vertebra the full character 4 (*b*) is shown. It is of interest to note also that the British Museum specimens of *Julis pavo*, *Coris cuvieri*, *Odax richardsoni* and *Scarus aurofrontus* agree with the Plymouth wrasses in the characters just referred to.

Concerning species of other divisions of the suborder Percoidea it may be said that *Ammodytes* still retains autogenous hypurals to the penultimate vertebra, whereas in *Callionymus* nothing appears to remain in the "tail" section of characters 4 (*a*), (*b*) or (*c*). On the other hand, the British Museum specimens of *Haplodactylus*, *Cirrhites*, *Chironemus*, *Chilodactylus* and *Latris*—all belonging to the division Cirrhitiformes—have a "tail" section which closely approximates to that of the Perciformes. *Gadopsis*, of the Gadopsiformes, resembles the Labrids, and *Trachinus* and *Ammodytes*, in having the antepenultimate hypural continuous with the centrum.

The "tail" section of the Blennioidea exhibits stages in specialization. The most generalized condition is seen in *Anarhichas* in which the penultimate vertebra carries autogenous hypurals, although not the antepenultimate. Even so, there is considerable departure from the perciform type in that the neural spine of the antepenultimate vertebra is not longer than those of preceding vertebrae, while that of the penultimate vertebra is quite stout and longer instead of being reduced. The species of *Blennius* have proceeded still further than *Anarhichas* in that the hypurals of the penultimate vertebra are no longer autogenous.

In the Gobioidea, as in *Blennius*, there is little or nothing to recall the generalized "tail" section. In the Mugiloidea, however, *Mugil* shows a great deal of it, and except that the hypurals of the antepenultimate vertebra are not autogenous, characters 4 (*a*), (*b*) and (*c*) are seen in full. In contrast, *Atherina*, of the same suborder, shows no agreement at all.



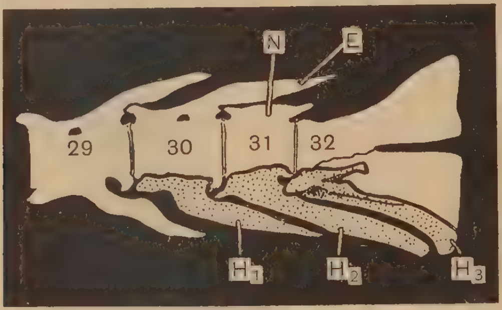
Text-fig. 14. Tail-end of *Labrus bergylta*. The antepenultimate hypural H_1 is continuous with the centrum, whereas H_2 and H_3 are autogenous. The epural E is long and the neural arch N is crested. The hypural H_3 does not bear a hook but articulates with the hypural posterior to it.

Order Scleroparei

In a paper on the classification of fishes of the order Scleroparei (or Loricati) Regan remarks that the most generalized family, the Scorpaenidae, is not very remote from the generalized percoids, such as the Serranidae. This is certainly borne out in a comparison of the backbone of *Sebastes marinus* or of *Scorpaena dactyloptera* with that of *Serranus cabrilla*. Save for the increased number of vertebrae in the two Scorpaenids, the fenestration of the parapophyses and of the haemal arches of the posterior caudal vertebrae, the agreement with

Serranus is very noticeable (cf. Plate VIII, fig. 1, and Plate XII, figs. 1 and 2). There is the same general form of the backbone as a whole and in its corresponding sections: the 1st neural spine is autogenous, the posterior parapophyses are closed, the shape of neural and haemal spines and of zygapophyses is very similar, while the "tail" section is of the typical percoid type described under characters 4 (*a*), (*b*) and (*c*) on p. 42. Moreover, as in *Serranus*, the vertebral characters have a very high degree of constancy.

The Triglidae, which Regan places next to the Scorpaenidae in the division Scorpaeniformes of the suborder Scorpaenoidea, are represented in the Plymouth material by the five gurnards, *Trigla lucerna*, *T. cuculus*, *T. gurnardus*, *T. lyra* and *T. lineata*. All of them have vertebral characters in common, not only with *Sebastes* and *Scorpaena*, but also with *Serranus*. The autogenous 1st neural spine is again present, the posterior parapophyses are bridged, and the "tail" vertebrae are of the typical percoid type (Text-fig. 15). *Trigla* further agrees with *Sebastes* and *Scorpaena* in that the 1st and 2nd neural spines are of equal height and convergent distally (Plate XII, fig. 3). There is, however, a well-defined "neck" section in this genus, made up of the first four or five vertebrae in which the backwardly directed dorsal post-zygapophyses are conspicuous. At the opposite end of the backbone the last eight or nine vertebrae show flattening and strengthening of the neural and haemal spines to form an attenuated skeletal root for the tail.



Text-fig. 15. Tail-end of *Trigla lyra*. The typical percoid condition is fully present.

In the other species of Scleroparei which have been examined, namely *Cottus bubalis*, *Agonus cataphractus*, *Cyclopterus lumpus* and *Spinachia spinachia*, most or all of the points of agreement with the percoid *Serranus* have disappeared. Indeed, it is difficult enough even to detect vertebral characters which will link these species with the more generalized members of their own order.

Order Heterosomata

In his monograph on the systematic revision of the flat-fishes Norman (1934) discusses the relationships of these fishes. He refers to the difference of opinion between authors as to whether the flat-fishes have been derived from a single stock, whether gadoid, zeoid or percoid, or from a number of stocks. Suffice it to say that Norman favours the view that the Heterosomata have arisen from a generalized percoid stock. But while he considers *Psettodes* to be the least specialized member of the order, he leaves open the possibility that the Soleidae and Cynoglossidae may have arisen from another part of the percoid stem. In this matter it is of considerable interest to note that the backbone of *Psettodes erumei* has the following characters in common with the generalized percoid:

Number of vertebrae $(n) = 24 = (10 + 14)$.
1st and 2nd vertebrae with well-developed, backwardly directed, superior posterior zygapophyses. 1st neural spine probably autogenous.
7th–10th vertebrae have closed haemal arches.
Haemal spine of 1st caudal vertebrae is not greatly different in length or breadth from those immediately following it.
Hypural of 23rd vertebra is autogenous from centrum.

But while *Psettodes* has at least this much in common with the generalized percoid, all the flat-fishes in the Plymouth material are far more specialized in vertebral form and reveal no very definite indication of possible percoid origin. Furthermore, the species examined can be easily segregated into four groups according to the following characters:

Whether the asymmetry is dextral or sinistral.
The relative height and disposition of the 1st neural spine.
The nature of the pre-caudal parapophyses.
The disposition of the series of apophyses arising from the middle line of the centra along the vertebral column.
The angles between the neural and haemal spines of the 1st caudal vertebra and the long axis of the vertebral column.

The grouping of the species thus affected and the characters of each group are as given on p. 48.

The data show that there is a pairing off between groups 1 and 2 (i.e. between subfamilies Pleuronectinae and Scophthalminae), and between groups 3 and 4 (i.e. between *Arnoglossus* and *Solea*). This is a matter of twofold interest. In the first place, it lends support to the possibility that the Heterosomata have been derived from more than one ancestral stock. In the second place, it reveals that *Arnoglossus* has more in common with *Solea* than with *Rhombus*, *Lepidorhombus*, *Phrynorhombus* and *Zeugopterus*, with which it is at present classified in the subfamily Scophthalminae of the family Bothidae. While it would be manifestly unwise to regard these two observations as anything more than tentative indications for more detailed study, they are both of no little interest and importance.

Group no.	Family	Subfamily	Genera	Species
1	Pleuronectidae	Pleuronectinae	*Reinhardtius*	*hippoglossoides*
			Hippoglossus	*hippoglossus*
			Hippoglossoides	*platessoides*
			Pleuronectes	*limanda* *platessa* *microcephalus* *cynoglossus* *flesus*
2	Bothidae	Scophthalminae	*Rhombus*	*maximus* *laevis*
			Lepidorhombus	*whiff-iagonis*
			Phrynorhombus	*norvegicus* *regius*
			Zeugopterus	*punctatus*
3	Bothidae	Bothinae	*Arnoglossus*	*laterna* *imperialis*
4	Soleidae	—	*Solea*	*solea* *lascaris* *variegata* *lutea*

Characters of each Group

Sinistral or Dextral	Group 1 Dextral	Group 2 Sinistral	Group 3 Sinistral	Group 4 Dextral
1st neural spine	Well developed, upstanding and of height exceeding that of cranium (Pl. XIII, fig. 1)	More slender than 2nd. Of same height as cranium, to which it is applied at its distal end (Pl. XIV, fig. 2)	Much reduced in size in comparison with 2nd	As in group 3 (Pl. XIII, fig. 2)
Pre-caudal parapophyses	Open	Open (Pl. XIV, fig. 3)	Closed	Closed (Pl. XIII, fig. 2)
Lateral apophyses	Restricted to caudal vertebrae	Restricted to caudal vertebrae (Pl. XIV, fig. 3)	Extend throughout whole column	Extend throughout whole column (Pl. XIII, fig. 3)
1st caudal vertebra	Neural and haemal spines set approximately at right-angles to long axis of centrum	Neural and haemal spines set obliquely to long axis of centrum. Forward angle of neural spine is an acute angle, but that of haemal spine is obtuse (Pl. XV, fig. 1)	Neural and haemal spines are both bowed backwards	Neural and haemal spines are both bowed backwards (Pl. XIII, fig. 2)

Despite the measure of agreement between species of group I (Pleuronectinae) and group 2 (Scophthalminae), there are very well marked differences between them. Members of the Pleuronectinae are not only dextral while those of the Scophthalminae are sinistral, but they have eggs without oil globules, whereas those of the Scophthalminae all possess oil globules. And as has already been mentioned on p. 41, this question of the phylogenetic significance of the oil globule is one which ought to receive closer attention. Furthermore, in the backbone itself, the sinistral Scophthalminae show a "facies" which is distinctive and different from that of the dextral Pleuronectinae, and one in which unequal development of vertebral characters on the upper (coloured) and lower (blind) sides of the body is more pronounced.

Before leaving the question of the group differences between the species of the Heterosomata it may be added that the Pleuronectinae can be subdivided by vertebral characters into three smaller groups as follows:

Reinhardtius *Hippoglossus*	*Hippoglossoides* *Pleuronectes limanda* *P. platessa* *P. flesus*	*P. microcephalus* *P. cynoglossus*

Coming now to consider the flat-fishes as a composite order, irrespective of external and internal relationship, it may be said that although there is an appreciable degree of variation in the number of vertebrae from individual to individual in every species, the number of pre-caudal vertebrae is always comparatively low in contrast with the number of caudals. Thus, in the Pleuronectinae, with the exception of *Reinhardtius* and *Hippoglossus*, the number of pre-caudals does not exceed thirteen (in *Reinhardtius* there are about nineteen and in *Hippoglossus* about sixteen), whereas the number of caudals may be as low as twenty-four to twenty-five in *P. flesus* and as high as at least forty-six in *P. cynoglossus* (forty-four in *Reinhardtius* and thirty-four to thirty-five in *Hippoglossus*). In the Scophthalminae the number of pre-caudals is ten or eleven in the six species exclusive of *Arnoglossus*, as compared with thirty to thirty-seven caudals. In *Arnoglossus* there are ten pre-caudals and thirty to thirty-four caudals, while in the four species of *Solea* there are nine to ten pre-caudals in contrast with twenty-nine to forty-one caudals.

Another feature in common among the species of Heterosomata is the tendency towards "bimodality" which is shown when a graph is plotted of the lengths of the successive vertebrae from one end of the backbone to the other. This tendency is perhaps most strongly shown by the species of the subfamily Scophthalminae.

Finally, it is worth drawing attention to the question of the external shape of flat-fishes in relation to that of the backbone, to which a brief reference was made on p. 20. There seems little doubt that in every flat-fish the long axis of the backbone is naturally arched in the pre-caudal region, more especially in species of the Scophthalminae. This arching results in, or is associated with, a displacement of the neural and haemal spines from a true symmetry with respect to the long axis of the column. This is clearly visible in the backbone of the turbot (Plate XV, fig. 1). It is seen that in the posterior-caudal region the neural and haemal spines are fairly symmetrically placed with respect to a series of ordinates at right angles to the long axis of the vertebral column. This symmetry, however, begins to break down as the middle of the backbone is approached from the tail-end, and in the 1st caudal vertebra the neural spine lies to the left of the ordinate while the haemal lies to the right. As already stated, the arching and asymmetry are most apparent in the species of the Scophthalminae.

Order Zeomorphi

The two species *Zeus faber* and *Capros aper* have very interesting backbones. Considering *Zeus* first, it is known that relationship with the Heterosomata has been suggested, and, at first sight, there are some surprising points of agreement between the backbone of the John Dory (Plate XVI, fig. 2) and that of, say, the turbot (*Rhombus maximus*) (cf. Plate XV, fig. 1). In both, there is natural arching of the vertebral column and the associated distortion of the angles made between the neural and haemal spines; there is bimodality in the length of the centrum along the column; the skeletal base of the caudal fin is of a conspicuously flattened form in both; the hinder part of the abdominal cavity has a bony wall, of which the strongly developed haemal spine of the 1st caudal vertebra is an important component.

But there are equally striking differences between the two species. In *Zeus* the parapophyses are closed and interlocked at their distal ends to form a kind of keel, whereas in *Rhombus* they are widely open and free from one another; lateral apophyses on either side of the caudal vertebrae are a strong feature of *Rhombus*, but they are entirely absent in *Zeus*; the neural arches are of an entirely different form in the two species; and whereas in *Rhombus*, as in all the other flat-fishes studied, there are twice as many caudal vertebrae as there are pre-caudals, in *Zeus* the number of caudals is only a vertebra or two more than the number of pre-caudals. One other difference is noteworthy, viz. in the form of the neural spine of the 1st vertebra. In *Zeus* the right and left elements of the spine are separate from one another, flattened, with their anterior edges closely applied to the cranium in such a way as to form a socket in which the 1st radial of the dorsal fin stands. In *Rhombus* the two halves of the neural spine are also in close association with the cranium, but they are closed together for the greater part of their length and certainly do not form a housing for the end of the fin radial.

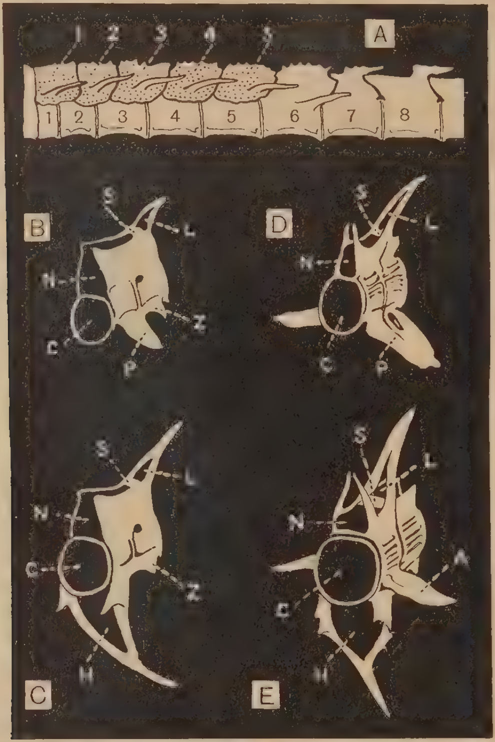
In these mixed circumstances of agreement on the one hand and disagreement on the other in vertebral characters, it cannot be said that the study of the backbone provides much confirmation of ancestral relationship between *Zeus* and the Heterosomata.

Turning to *Capros aper*, the other member of the order Zeomorphi, it is of interest to find that its backbone has a number of characters in common with the percoid type. There are ten pre-caudal vertebrae, of which the 7th to the 10th have bridged parapophyses. There are twelve caudals (i.e. two less than in the generalized percoid) but the "tail" section composed of the final three is reminiscent of the percoid. Thus, the hypurals of the antepenultimate and penultimate vertebrae, as well as the foremost hypural of the terminal (urostylar) segment are autogenous, while the latter is hooked. *Capros* agrees with *Zeus* in the application of the 1st neural spine to the cranium to form a socket in which the first radial of the dorsal fin may stand. It may also be observed in passing that the species has succeeded in developing a most ingenious mechanism for locking the spines of the dorsal and pelvic fins in an erected position with respect to the body. This is not the place to describe the locking structures, but they would well repay close examination by any worker interested. Indeed, the study of locking devices among fishes in general, particularly among fishes of the orders Percomorphi and Scleroparei, in which these occur more frequently than might be realized, is one of no little interest. The engineering problems raised, the ways in which the different fishes have solved them, and the manner in which the bony structures concerned are developed, are all matters on which further information is desired.

Order Apodes

In addition to the orders considered in the foregoing pages, there are several which are represented in the Plymouth material by one or two species only. The first of these is the Apodes, represented by *Anguilla anguilla* and *Conger conger*. The backbones of these are readily distinguishable from one another, although they agree in having autogenous neural arches on certain of the anterior pre-caudal vertebrae; in the separate housings for the longitudinal ligament and spinal cord; in the convex anterior face of the 1st vertebra; and in the general form of the last vertebra.

In *Anguilla anguilla* an interesting condition is presented by the neural arches of the first eight vertebrae. Those of vertebrae 1–5 are autogenous from the centrum and bear on either side a backwardly directed hook-like process (Text-fig. 16A). Above the spinal cord the arches of the two sides come together in a median crest, in shape resembling that of a cockscomb. The posterior end of the neural arch of each of these five vertebrae overlays the anterior end of the neural arch of the succeeding vertebra. In the 6th vertebra the neural arch becomes fused with the centrum, instead of being autogenous from the centrum. Nevertheless, like the five vertebrae preceding it, it bears the lateral hook and the median cockscomb, and its posterior end overlays the anterior end of the 7th. The 7th vertebra is unique in that its neural arch is overlain at both ends—anteriorly, by the posterior end of the neural arch of the 6th, and posteriorly, by the anterior end of the arch of the 8th. It bears no lateral hook, but the median cockscomb is still present. The 8th vertebra shows a transition stage towards the more typical pre-caudal condition in which the neural arch bears a closed, supplementary arch at its posterior end, through which passes the longitudinal ligament. Anteriorly, the neural arch overlays the posterior end of the preceding neural arch.



Text-fig. 16. A, *Anguilla anguilla*. First eight vertebrae viewed from side, to show the hook-bearing, autogenous neural arches on vertebrae 1–5. Vertebra 6 has its neural arch fused to the centrum, and the lateral hook arises more ventrally. The neural arch of vertebra 7 is interlocked by those of vertebrae 6 and 8. B, *Anguilla anguilla*. Typical pre-caudal vertebra (cf. with that of *Conger* in Fig. D). C, *Anguilla anguilla*. Typical caudal vertebra (cf. with that of *Conger* in Fig. E). D, *Conger conger*. Typical pre-caudal vertebra. E, *Conger conger*. Typical caudal vertebra.

Abbreviations used in Figs. A–E: *N*, neural canal; *C*, anterior end of centrum; *H*, haemal canal; *P*, parapophysis; *A*, lateral apophysis; *Z*, ventral post-zygapophysis; *S*, transverse septum above neural canal; *L*, ligamentary canal.

In Text-figs. 16B and C typical pre-caudal and caudal vertebrae are depicted. It will be observed that the latter are entirely without lateral apophyses, which are so conspicuous a feature in *Conger conger* (see below).

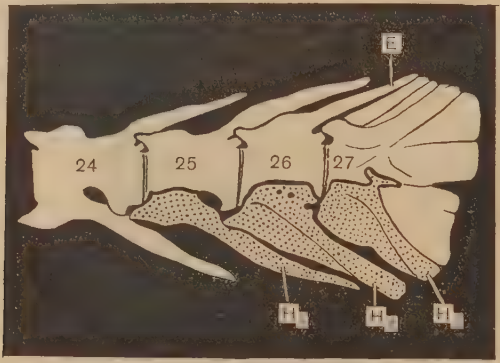
The backbone of *Conger conger* (Text-figs. 16 D and E) is distinguishable from that of *Anguilla anguilla* throughout its length. Anteriorly, the first sixteen or seventeen vertebrae have autogenous neural arches surmounted by conspicuous, laterally flattened neural spines of approximately equal height. In contrast with *Anguilla*, only the 2nd vertebra appears to bear a conspicuous "rib"-bearing hook at the base of the neural arch, although a reduced form of hook-like process is present on the 3rd to about the 8th. The parapophyses on either side of the 2nd to the 5th or 6th are duplicate structures, one above the other, which, on the 6th or 7th, become merged to form a single process. Proceeding along the backbone, an obvious difference from *Anguilla* is the progressive change in form of the parapophyses in the pre-caudal region and the apparent fusion of these processes with the ventral post-zygapophyses, which, in *Anguilla*, retain their separate identity. Towards the end of the pre-caudal section of the backbone there is the first evidence of the separation of each parapophysis into an upper apophyseal process and a lower parapophysis of the normal type. In the first of the caudal vertebrae this separation is complete, the apophysis projecting at right angles from the centrum, immediately above the closed haemal arch. The series of these lateral apophyses extends backwards over many vertebrae and serves as a readily distinguishable feature of difference between *Conger* and *Anguilla*. The backbone of *Conger* is further distinguishable from that of *Anguilla* by the heavy sculpturing of the surfaces of the centra throughout the column.

Order Synentognathi

Scombresox saurus and *Belone belone* have been examined. Both backbones, consisting of a large number of vertebrae, have numerous points in common. In the long pre-caudal section, widely open but short rod-like parapophyses are present on each vertebra from the 1st backwards. Except on the most anterior and most posterior vertebrae, where they are flattened, the neural spines throughout the whole column are slender and spine-like. A characteristic feature in both species is the disproportionately large size of the dorsal pre-zygapophyses, although here there is a sharp distinction between the two species. In *Belone* these zygapophyses are flattened triangular plates, one side of which is applied to the neural spine of the preceding vertebra. In *Scombresox* they are curiously elaborate in form and separated from the neural spine of the preceding vertebra by posterior zygapophyseal processes, with which they interlock. *Scombresox* is further distinguished from *Belone* by the presence of a well-differentiated "tail" section in which the neural and haemal spines are strengthened and lay back along the length of the column. It is of interest to note that the neural arch of the penultimate vertebra is reduced to a low crest not unlike the condition in percoids. It is possible, although the point is subject to confirmation on further material, that the hypural of the penultimate vertebra is autogenous in *Scombresox*.

Order Discocephali

Two specimens of the interesting sucking fish, *Remora remora*, have been obtained at Plymouth. The backbone comprises twenty-seven vertebrae, made up of twelve pre-caudals and fifteen caudals. In the pre-caudal region, the neural arches of vertebrae 1–3 form a low-lying crest by the suppression of the neural spines, and thus afford a seating for the skeleton of the sucker. Rather long, rod-like parapophyses stand out laterally from each of the anterior pre-caudal vertebrae, but the length decreases and the rods turn downwards in the posterior pre-caudals. A noticeable feature of the 10th, 11th and 12th vertebrae is the presence of rather long, downwardly directed postero-ventral zygapophyses. In the caudal region the final three vertebral segments form a "tail" section in which the hypurals of both antepenultimate and penultimate vertebrae are autogenous, and in which the foremost hypural of the terminal segment is also autogenous and bears a hook (Text-fig. 17). The epurals of the antepenultimate vertebrae are elongate and enter into the skeleton of the caudal fin. It need hardly be said that these characters of the "tail" section are reminiscent of the generalized percoid.



Text-fig. 17. Tail-end of *Remora remora*. Hypurals H_1, H_2 and H_3 are autogenous, H_3 is hooked, but the neural arch of 26th vertebra bears elongate epural, *E*.

Order Plectognathi

Two specimens of *Balistes capriscus* have been examined, both of which had eighteen vertebrae, made up of eight pre-caudals and ten caudals. Superficially, the backbone of this species recalls that of the John Dory (*Zeus*). There is the same natural curvature of the column, with the heavy skull set at an angle at the anterior end; the posterior parapophyses and the haemal spine of the first caudal vertebra together form a stout posterior wall to the abdominal cavity; the superior anterior zygapophyses are strongly developed. But at both head and tail-ends *Balistes* differs greatly from *Zeus*, although, here again, there is some agreement in that the 1st neural spine is closely applied to the cranium. In the first five vertebrae of *Balistes*, however, the neural spines are clearly modified in shape and set to receive the elements of the complex "trigger" mechanism which characterizes the species. The 2nd to 5th vertebrae also bear open parapophyses. At the opposite end, the penultimate vertebra has autogenous hypurals, which, like the epurals, constitute elongated and strengthened skeletal supports for the caudal fin.

Two small specimens of the sunfish *Mola mola* were caught off Plymouth and brought to the Laboratory in July 1937. Their skeletons were prepared by dissecting away the tough, blubbery carcase and disarticulating the backbone, vertebra by vertebra, having first noted the relation of each with respect to the fin-radials. In general form and arrangement the two backbones were very similar to that portrayed by Steenstrup & Lütken under *M. rotunda* (1898, plate II), but they differed in several important characters. Thus, both had nine caudal vertebrae in a total of seventeen (=8+9), instead of eight in a total of sixteen (=8+8). Vertebrae 1–4 form a distinct group in which the neural spines of the right and left side do not meet above the spinal cord to form a closed neural canal. Instead, the latter is open above as a narrow longitudinal slit. The neural spines of the 1st vertebra project forward to form occipital articulation with the skull on either side of a median occipital crest. The 2nd vertebra is unusual for the fore-and-aft projections of the neural arches and spines which overlie the centra of the 1st vertebra in front and the 3rd vertebra behind, and make a snug fit with the proximal parts of the neural arches of these vertebrae. The 3rd and 4th vertebrae have short, backwardly directed neural spines which, with those of vertebra 1 and 2, form a beautifully interlocked and low-lying neural crest.

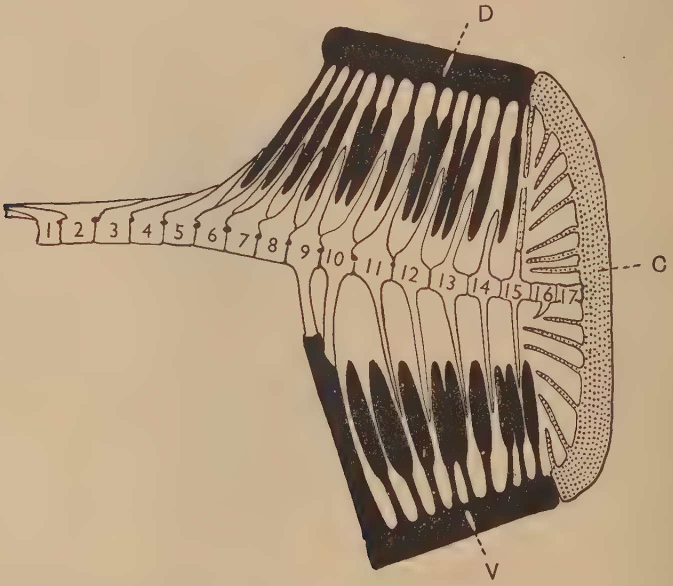
Vertebrae 5–8 form a second group with distinctive characters. Like the first four vertebrae they are without haemal arches, but unlike them they have a closed neural canal which penetrates a single, solid neural spine of considerable length and stability. Each of these neural spines is interlocked with the anterior radials of the dorsal fin.

Vertebrae 9 and 10 are the first of the caudals. Their very long haemal spines come together distally to lie together within the semi-tubular and massive anterior radial element of the anal fin. In both vertebrae, however, the right and left haemal spines retain their separate identity throughout their length. Dorsally, they have single, solid neural spines, interlocking with the dorsal radials.

Vertebrae 11–15 agree in having solid neural spines, penetrated by a tubular neural canal which becomes reduced to pin-size diameter in the 15th. Ventrally, the haemal arches are closed and prolonged distally into single haemal spines. Both neural and haemal spines interlock with fin radials, those of the 15th entering into the support of the caudal fin radials.

There remain the two terminal vertebrae, nos. 16 and 17. Of these, the former consists of little more than a cylindrical centrum bearing a short haemal process, while the latter has a centrum without processes at all.

The relation of the neural and haemal spines in general to the radials of the dorsal, anal and caudal fins is shown diagrammatically in Text-fig. 18. A comparison with Steentrup's figure shows some difference in this respect, particularly at the hinder end of the backbone, where the radials of the caudal fin are concerned.



Text-fig. 18. *Mola mola.* The backbone in relation to the endoskeleton of the dorsal, anal and caudal fins. (Diagrammatic.) *D*, radial skeleton of dorsal fin (solid black); *V*, radial skeleton of anal fin (solid black); *C*, radial skeleton of caudal fin (stippled).

Order Pediculati

Lophius piscatorius has a backbone which is composed of a series of vertebral segments compactly interlocked to form a skeletal rod between head and caudal fin. The neural and haemal processes are comparatively short and robust, and strongly flexed backwards along the length of the column. Indeed, in the precaudal region, the parapophyses lie almost parallel with the long axis through the centra, and overlap from front to back to form a continuous ventral face beneath the centra. The actual bone substance of the vertebrae is of a spongy nature, with the result that the whole backbone, when dried, is surprisingly light in weight. The hindermost vertebrae comprise a stout base for the caudal fin, the penultimate vertebra possessing particularly heavy epurals which are depressed to lie parallel to the long axis. Considering the massive form of the body of *Lophius*, the backbone is something of a surprise in its almost unrelieved compactness.

CONCLUDING REMARKS

The major conclusion which has been reached as the result of the work surveyed in the foregoing pages is that almost every one of the different aspects of vertebral variation discussed is a worthy subject for intensive study, likely to yield highly interesting and useful results. Of actual material for these researches there can be no possible shortage, since every fish in the sea, regardless of species, is a potential source of fresh information. In the present paper an endeavour has been made to set out in bare outline the manifold problems awaiting full investigation. No claim is made that the observations therein made are new, not having been previously observed and described. As stated in the introduction, the work was prompted by the desire to avoid error and misunderstanding in the treatment and interpretation of statistical data on vertebral variation among populations of economically important fishes. It has led to a radical change of outlook and a much increased consciousness of the need for extreme care and caution in population studies of the kind referred to. More than this, it has convinced the author that the study of the piscine vertebral column brings an investigator hard up against the great fundamental questions in zoology, and is therefore deserving of intensive study in the immediate future.

REFERENCES

BARRINGTON, E. J. W., 1937. The structure and development of the tail in the plaice (*Pleuronectes platessa*) and the cod (*Gadus morrhua*). *Quart. Journ. Micr. Soc.*, Vol. 79, pp. 447–69.

BATESON, W., 1894. *Materials for the Study of Variation.* London: Macmillan and Co.

COLE, F. J. & JOHNSTONE, J., 1901. *Pleuronectes* (the plaice). *L.M.B.C. Memoir* VIII.

FORD, E. & BULL, H. O., 1926. Abnormal vertebrae in the herring. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 509–17.

FORD, E., 1930. Herring investigations at Plymouth. VIII. The transition from larva to adolescent. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 723–52.

—— 1931*a*. Growth in length during the transition from larva to adolescent in the pilchard and sprat. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 977–85.

—— 1931*b*. Changes in length during the larval life and metamorphosis of the freshwater eel (*Anguilla vulgaris* Turt.). *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 987–1009.

—— 1933. The "number of vertebrae" in the herring and its variation. *Journ. Cons. Int. Explor. Mer*, Vol. VIII, pp. 211–22.

GRAY, J., 1933*a*. *The Muscular Movements of Fishes.* Royal Institution of Great Britain.

—— 1933*b*. Studies in animal locomotion. I, II and III. *Journ. Exp. Biol.*, Vol. X, pp. 88–104 and 386–400.

Kändler, R., 1932. Unsicherheiten bei Bestimmung der Wirbelzahl infolge Verwachsungserscheinungen. *Journ. Cons. Int. Explor. Mer*, Vol. vii, pp. 373–85.

Kishinouye, K., 1923. Contributions to the comparative study of the so-called Scombroid fishes. *Journ. Coll. Agric., Imp. Univ. Tokyo*, Vol. viii, pp. 293–475.

Kyle, H. M., 1926. *The Biology of Fishes*. London: Sidgwick and Jackson, Ltd.

Norman, J. R., 1935. *Fishes*. List of British Vertebrates, British Museum (Natural History), pp. 40–66.

—— 1934. *Monograph of the Flatfishes*, Vol. i. British Museum (Natural History), London.

Schmidt, J., 1921. Racial investigations. VIII. The numerical signification of fused vertebrae. *C.R. Trav. Carlsberg*, Vol. xiv, No. 16.

Schnakenbeck, W., 1931. Zum Rassenproblem bei den Fischen. *Zeitschr. f. Wiss. Biol.*, Abt. A, *Zeitschr. f. Morphol. u. Ökol. d. Tiere*, Band 21, Heft 3/4, pp. 409–566.

Steenstrup, J. & Lütken, Chr., 1898. Bidrag til Kundskab om Klump-eller Maanefiskene (Molidae). *Mémoires de l'Académie Royale des Science et des Lettres de Danemark, Copenhague*, 6me série, Section des Sciences, t. ix, No. i.

Thompson, D'Arcy W., 1917. *On Growth and Form*. Cambridge: University Press.

Whitehouse, R. H., 1910. The caudal fin of the Teleostomi. *Proc. Zool. Soc. London*, pp. 590–627.

EXPLANATION OF PLATES

Plate I. *Alosa alosa*

Fig. 1. View of ventral surface showing last pair of autogenous parapophyses on the 17th vertebra, and the first closed haemal arch on the 18th.

Fig. 2. View of left side showing last pair of autogenous parapophyses on 17th vertebra. Note also the autogenous neural arches in this region of the backbone.

Fig. 3. View of left side showing the last pair of autogenous neural arches on the 23rd vertebra, and the first appearance of the spine-like pre-zygapophyseal process on the haemal arch of the 25th vertebra.

Plate II

Figs. 1 and 2. *Gadus callarias*. Views of right side and ventral surface of the post-cranial or "neck" section of the backbone. Note the lateral position of the dorsal pre-zygapophyses on the first three vertebrae, and the locking of the 4th vertebra in front and behind.

Fig. 3. *Gadus virens*. View of right side of post-cranial or "neck" section. Compare the relative heights of the neural spines of vertebrae 1, 2 and 3 with those of the corresponding vertebrae in *G. callarias* (fig. 1).

Fig. 4. *Molva molva*. Ventral view of post-cranial section of backbone.

Plate III

Fig. 1. *Gadus luscus*. View of right side of pre-caudal section of backbone, for comparison with corresponding views of other species illustrated in figs. 2, 3 and 4. Note that the 1st neural spine is of the same height as, and closely applied to, the supra-occipital. The 2nd and 3rd neural spines are shorter than the 1st.

Fig. 2. *Gadus pollachius*. Corresponding view. Note that 2nd and 3rd neural spines are longer than 1st. The small arrow points to the open groove in the neural arch, for the passage of the spinal nerves.

Fig. 3. *Mora mediterranea*. Corresponding view. The 1st neural spine is of characteristic appearance, but still in typical association with the supra-occipital as in *Gadus*.

Fig. 4. *Merluccius merluccius*. Corresponding view. The 1st neural spine is a bifurcate structure, but still in typical association with the supra-occipital. The neural arches and spines of the pre-caudal vertebrae are of characteristic appearance. The scroll-like parapophyses are also noteworthy.

Plate IV

Fig. 1. *Gadus merlangus.* Ventral surface in pre-caudal region. Note the typical "neck" of four vertebrae. Lateral apophyseal processes are present between the parapophyses.

Fig. 2. *Urophycis blennoides.* Corresponding view. Note the "neck" of four vertebrae and the form of the parapophyses. The deeply-pitted ventral surfaces of the pre-caudal centra, and the large haemal ring of the 1st caudal vertebra, are clearly shown.

Fig. 3. *Merluccius merluccius.* Corresponding view. The "neck" and scroll-like parapophyses are of a striking and characteristic appearance.

Fig. 4. *Gadus aeglifinus.* Corresponding view. The neck is short. The parapophyses are large, forming a regular canopy. The characteristic shape of the haemal arch of the 1st caudal vertebra is observable (indicated by arrow).

Plate V

Fig. 1. *Onos* sp. Three-barbed rockling, form A (see p. 11 of text). Note that nerve foramina are present on vertebrae 4–12, but that on the 13th and subsequent vertebrae their place is taken by open grooves.

Fig. 2. *Gadus luscus.* To show open parapophyses on pre-caudal vertebrae, and well-developed "haemal funnel" at front end of caudal region.

Fig. 3. *Gadus pollachius.* Similar view to fig. 2.

Plate VI

Fig. 1. *Urophycis blennoides.*
Fig. 2. *Gadus virens.*
Fig. 3. *Mora mediterranea.*
Fig. 4. *Gadus pollachius.*

Showing variation in the form of the tail-end of the backbone.

Plate VII. *Morone labrax*

Fig. 1. View of left side (see p. 32 of text).

Fig. 2. Enlarged view of supra-occipital to show growth rings.

Fig. 3. Tail-end (for comparison with Text-fig. 1 on p. 7).

Plate VIII

Fig. 1. *Serranus cabrilla.* The autogenous neural spine of the 1st vertebra is missing, but its position is indicated by the arrow. Growth rings on the supra-occipital are just visible.

Fig. 2. *Pagellus centrodontus.* View of ventral surface to show the walled blood tract along the pre-caudal vertebrae.

Plate IX

Fig. 1. *Scomber scombrus.* General view of right side. Note the first appearance of a haemal arch on the 10th vertebra. A drawing of the "tail-section" from vertebrae 26 to 31 is given in Text-fig. 4 on p. 8.

Fig. 2. *Caranx trachurus.* General view of right side. Note the enlarged intervals between the neural spines of 2nd and 3rd vertebrae, and of 11th and 12th. The haemal arch in this specimen is first foraminated on the 15th vertebra. The "tail-section", comprising vertebrae 20–24 is shown diagrammatically in Text-fig. 3 on p. 8.

Fig. 3. *Katsuwonus pelamys.* View of tail-end.

Fig. 4. *Caranx trachurus.* Enlarged view of anterior end to show autogenous neural spine to 1st vertebra, and the characteristic widening of the interval between neural spines 2 and 3 to receive the first dorsal radial.

Plate X. *Labrus bergylta*

Fig. 1. Enlarged view of the haemal arch of the 1st caudal vertebra to show the growth rings.

Fig. 2. Ventral surface of anterior vertebrae to show the large backwardly directed apophyseal processes overlapping adjacent vertebrae.

Plate XI. *Mugil* spp.

Fig. 1. *Mugil chelo*. (Thick-lipped grey mullet.) Left side showing the characteristic form of the neural spines of the first seven vertebrae, and the "hook" at the posterior end of the 2nd (indicated by arrow).

Fig. 2. *Mugil chelo*. Abdominal region. Note the first appearance of the ventral post-zygapophysis on the 9th vertebra.

Fig. 3. *Mugil* spp. (Thin-lipped grey mullet.) Abdominal region. Note that the ventral post-zygapophysis is present on the 8th vertebra (cf. *M. chelo* in fig. 2). The reticulated surfaces of the vertebral centra form a contrast with the condition in *M. chelo* as shown in fig. 2.

Plate XII

Fig. 1. *Sebastes marinus*. View of right side. For details see Text-fig. 9 on p. 19 of text.

Fig. 2. *Scorpaena dactyloptera*. View of right side. For details see Table on p. 33 of text.

Fig. 3. *Trigla lyra*. View of left side. The arrow is pointing to the neural spines of vertebrae 1 and 2, which are of equal height and brought into adjacency at their distal ends.

Fig. 4. *Trigla lyra*. Ventral view to show the flattened distal ends of the haemal arches on vertebrae 9–12 (see p. 12 of text).

Plate XIII

Fig. 1. *Pleuronectes flesus*. Pre-caudal region. Note the upstanding neural spine of the 1st vertebra, clear of the skull. The parapophyses are open on the pre-caudals.

Fig. 2. *Solea solea*. Pre-caudal region. The neural spines of the 1st vertebra are much reduced, with their distal ends open. The haemal arches from the 5th vertebra onwards are closed.

Fig. 3. *Solea solea*. Ventral view of pre-caudal region to show closed haemal arches. Lateral apophyses are present on pre-caudal vertebrae as well as on caudal.

Plate XIV. *Lepidorhombus whiff-iagonis*

Fig. 1. View of left side.

Fig. 2. Front end viewed from left side. The neural spine of the 1st vertebra is in contact with the cranium and of a similar height. The lateral apophyses on the centra from vertebra 11 backwards are clearly shown.

Fig. 3. Ventral view of front end. Note the open parapophyses on vertebrae 5–10. The lateral apophyses from vertebra 11 backwards are larger on the left side than on the right.

Plate XV. *Rhombus maximus*

Fig. 1. View of left side. The dotted line *AB* has been inserted to show the asymmetry of the neural and haemal spines of the 1st caudal vertebra with respect to the long axis of the centrum. The bowing of the long axis of the backbone at the anterior end is well marked.

Fig. 2. Enlarged view of caudal peduncle to show growth rings on the flattened hypurals.

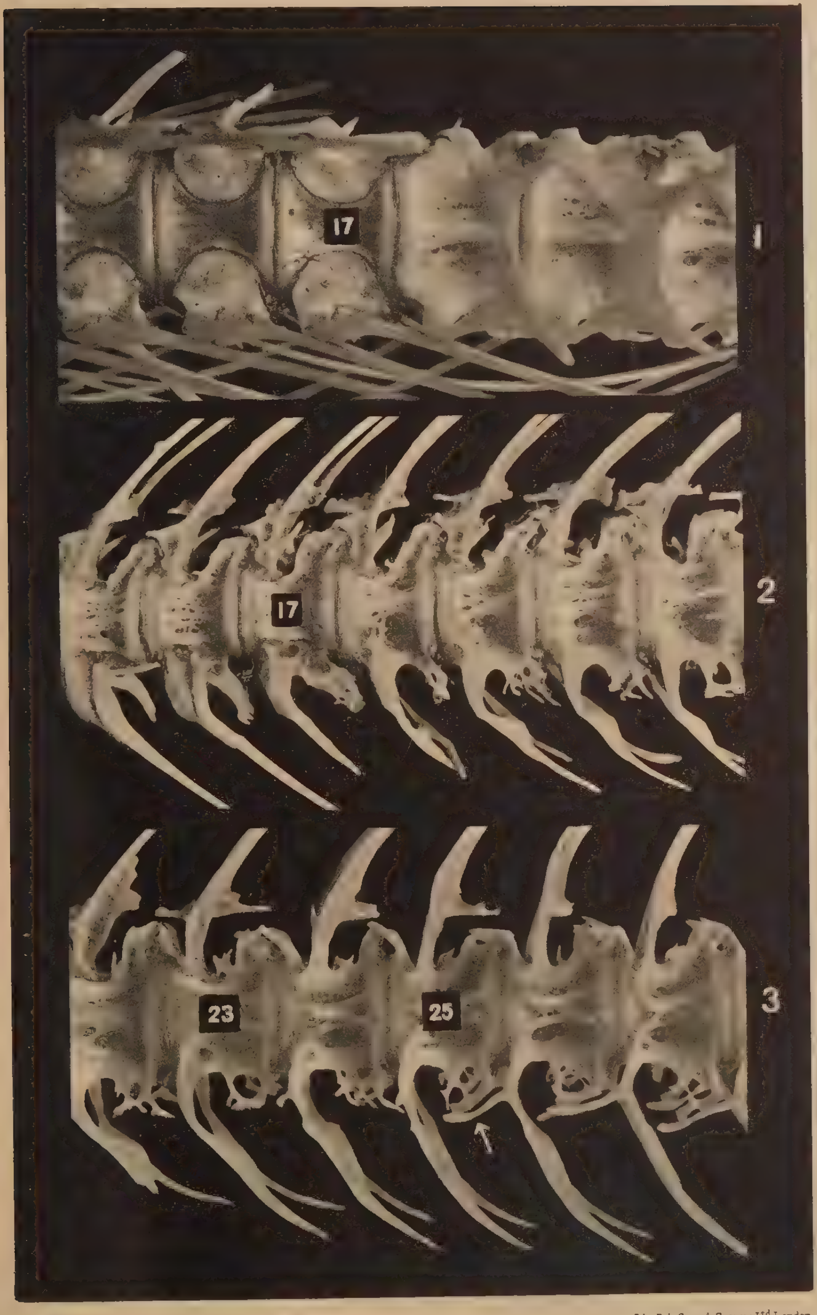
Fig. 3. Enlarged view of anterior end of backbone to show the form and position of the 1st neural spine in association with the cranium. Note also the open parapophyses.

Plate XVI

Fig. 1. *Balistes capriscus*. The modified form of the anterior neural spines is to be associated with the support and functioning of the "trigger" mechanism. Note that the hypural of the 17th (penultimate) vertebra is autogenous from the centrum.

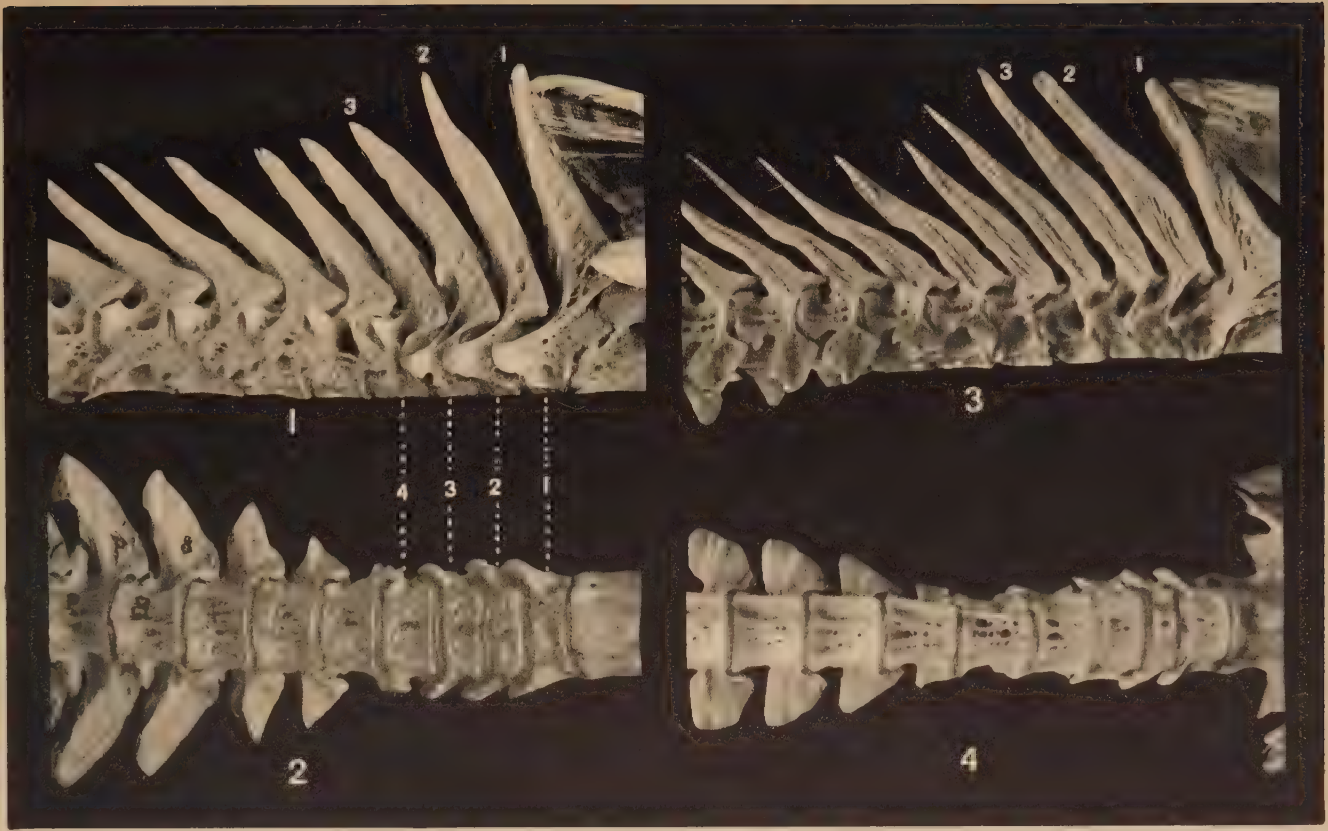
Fig. 2. *Zeus faber*. View of right side. A point of especial interest is the arrangement of the anterior neural spines in pairs—3 and 4, 5 and 6, 7 and 8.

Fig. 3. *Zeus faber*. Enlarged view of skull to show growth rings (indicated by arrow).


17
1
17
2
23
25
3

John Bale Sons & Curnow, L^td London

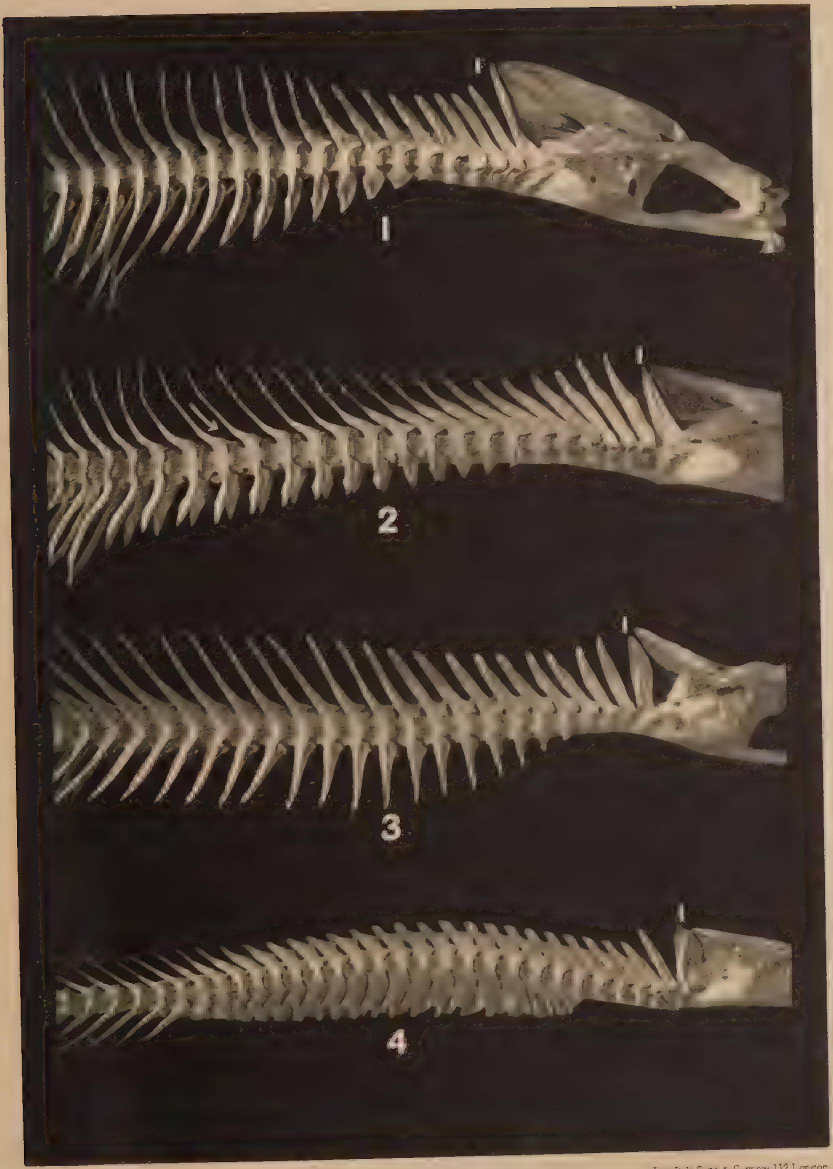
Figs. 1, 2 and 3. *Alosa alosa.*


1
2
3
1
2
3
3
1
2
3
4
2
4

John Bale Sons & Curnow, L^{td} London

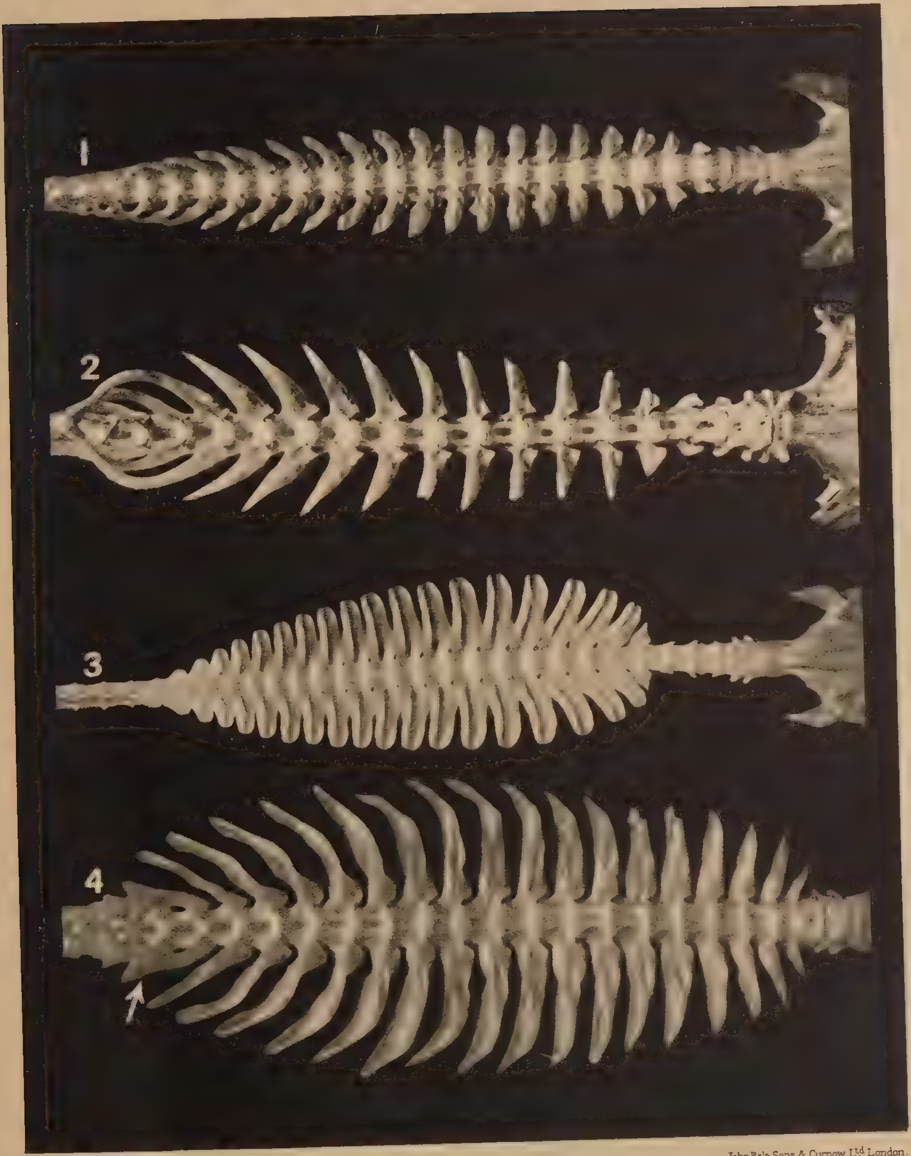
Figs. 1 and 2. *Gadus callarias.* Fig. 3. *Gadus virens.* Fig. 4. *Molva molva.*

PLATE III.



John Bale Sons & Curnow Ltd London

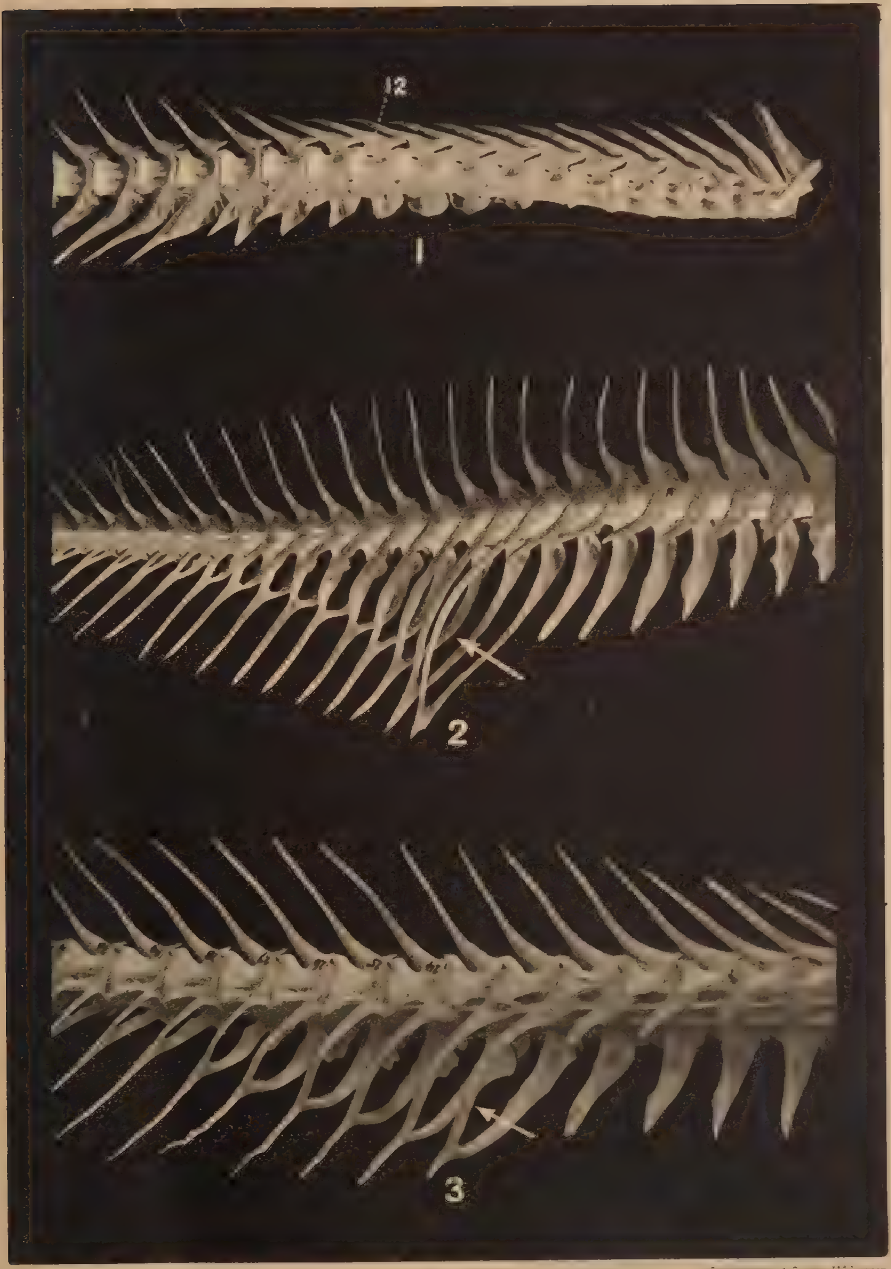
Fig. 1. *Gadus luscus.*
Fig. 2. *Gadus pollachius.*
Fig. 3. *Mora mediterranea.*
Fig. 4. *Merluccius merluccius.*



John Bale, Sons & Curnow, L^td London.

Fig. 1. *Gadus merlangus.*
Fig. 2. *Urophycis blennoides.*
Fig. 3. *Merluccius merluccius.*
Fig. 4. *Gadus aeglifinus.*

PLATE V.

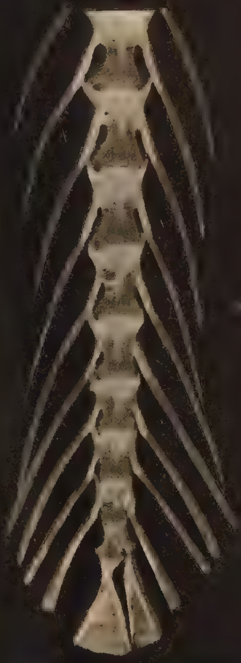


John Bale Sons & Curnow, Ltd London

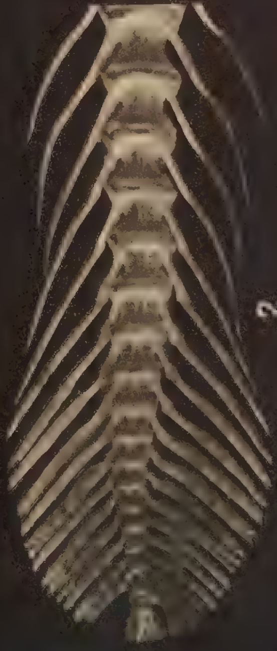
Fig. 1. *Onos sp.* (3-barbed rockling, form A).

Fig. 2. *Gadus luscus.* Fig. 3. *Gadus pollachius.*

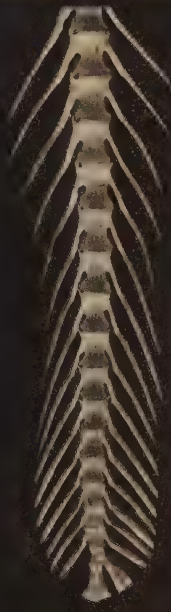
PLATE VI.



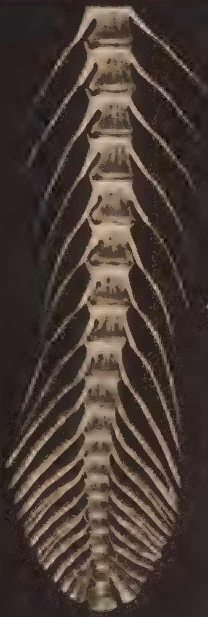
1



2



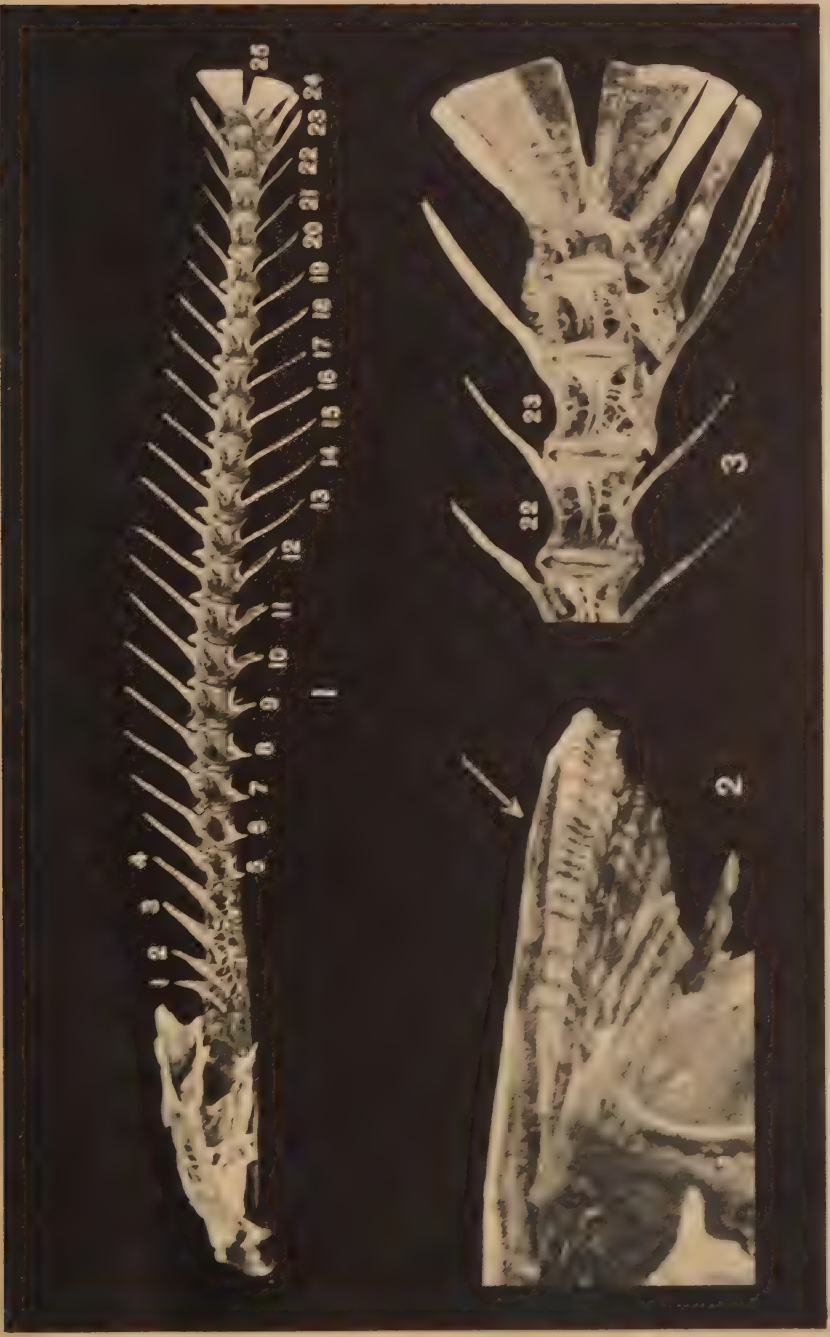
3



4

Fig. 1. *Urophycis blennoides.*
Fig. 2. *Gadus virens.*
Fig. 3. *Mora mediterranea.*
Fig. 4. *Gadus pollachius.*

John Bale, Sons & Curnow, L^td London


1
2
3
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
22
23

Figs. 1, 2 and 3. Morone labrax.

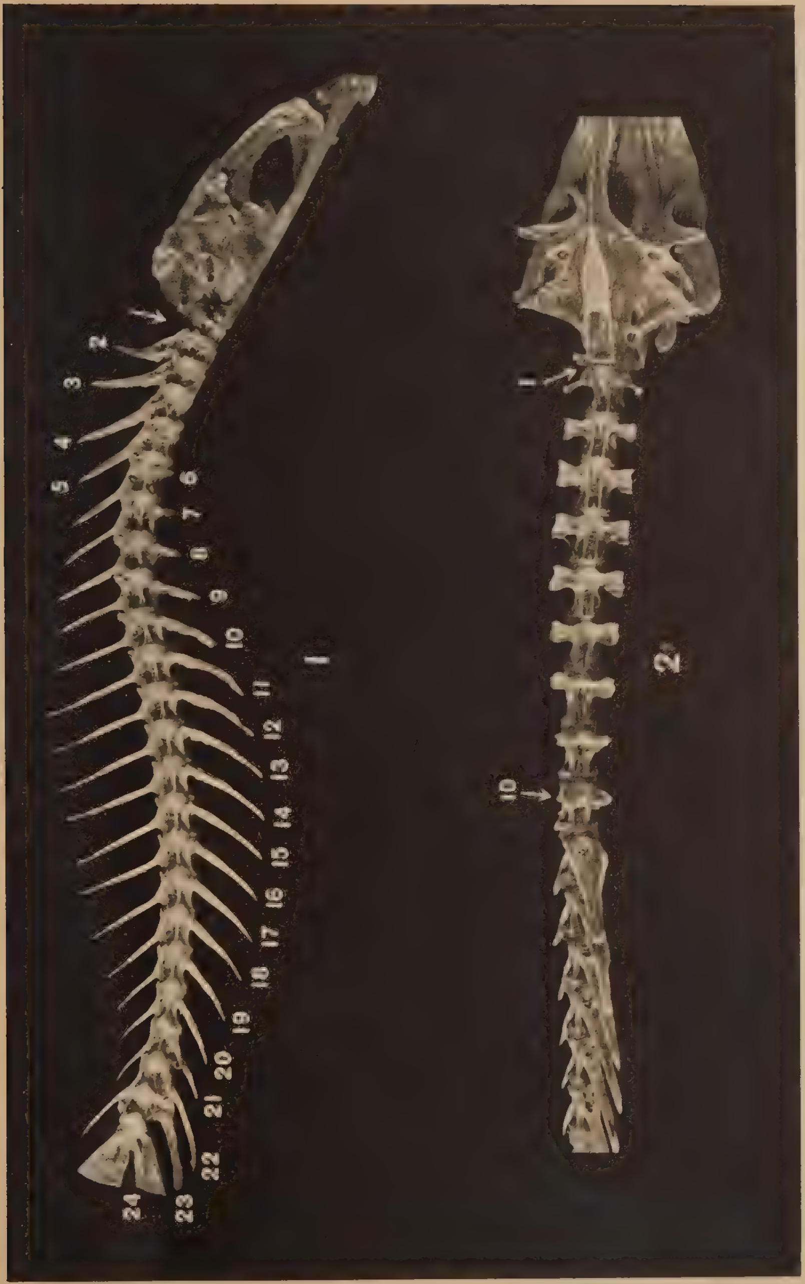
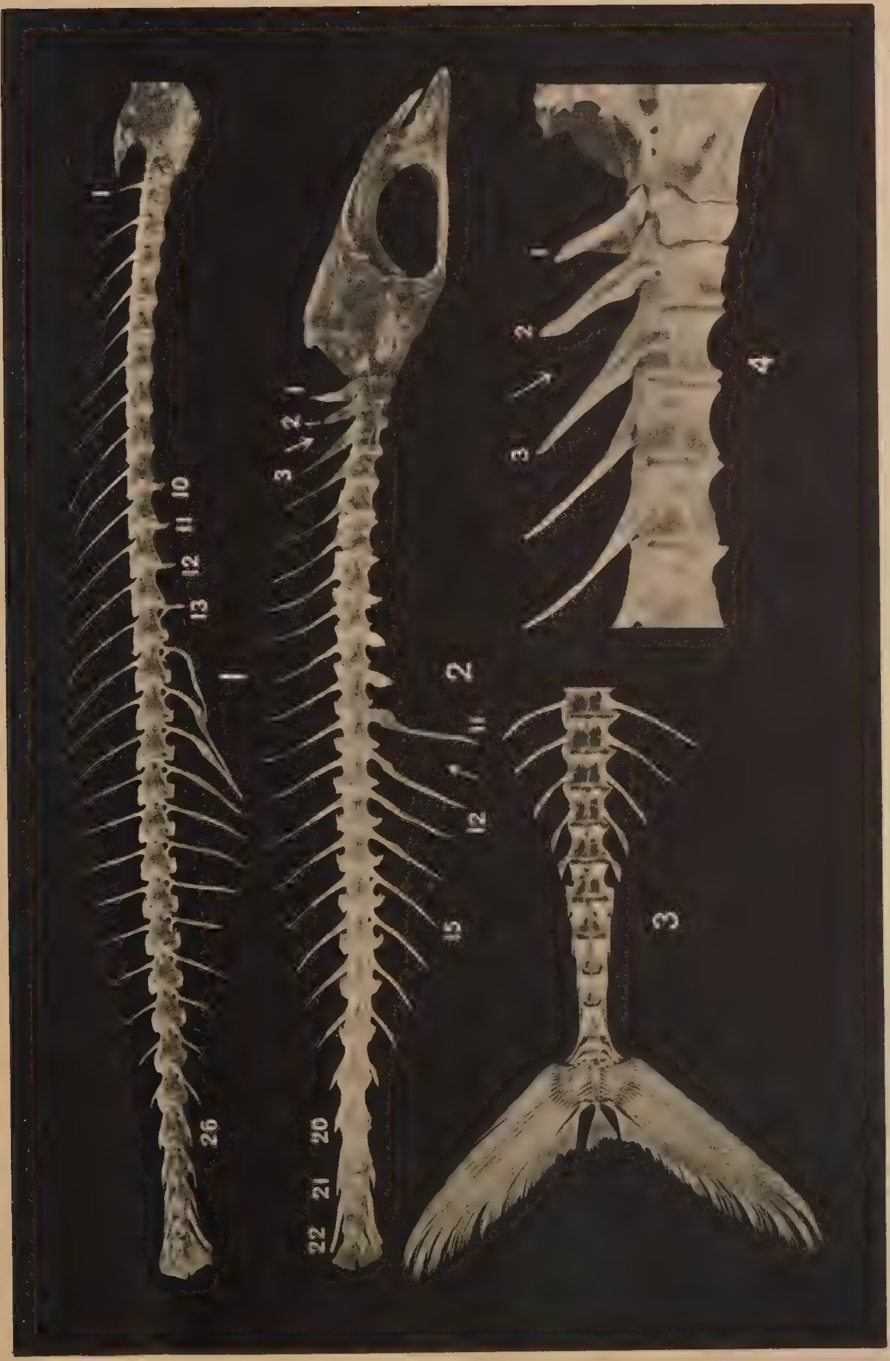
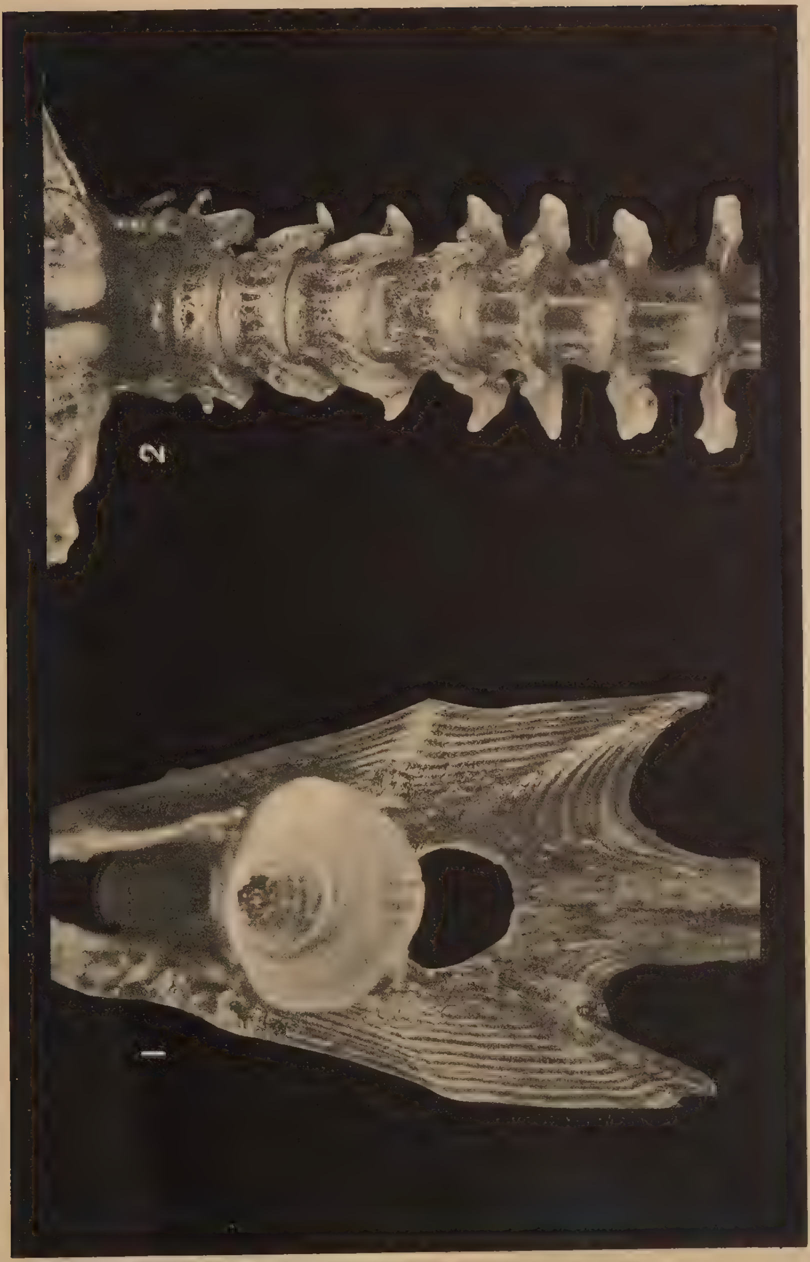

1
2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
1
10

Fig. 1. *Serranus cabrilla.* Fig 2. *Pagellus centrodontus.*


1
10
11
12
13
1
26
1
2
3
2
11
12
15
20
21
22
1
2
3
4
3

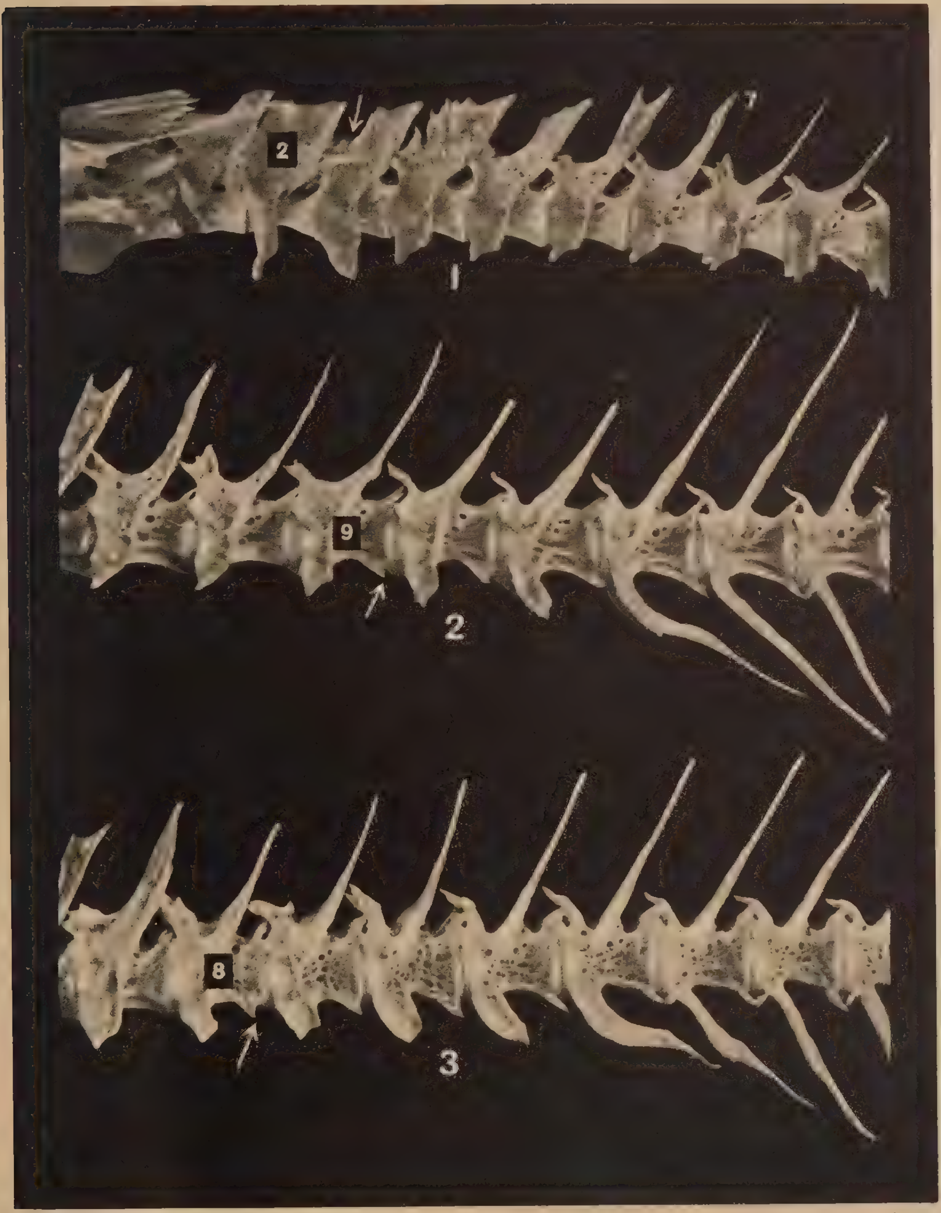
John Bale, Sons & Curnow Ltd London.

Fig. 1. *Scomber scombrus.* Fig. 2. *Caranx trachurus.*
Fig. 3. *Katsuwonus pelamys.* Fig. 4. *Caranx trachurus.*



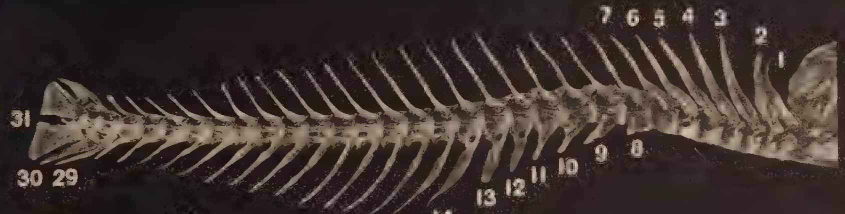
John Bale Sons & Curnow, Ltd London

Figs. 1 and 2. *Labrus bergylta.*

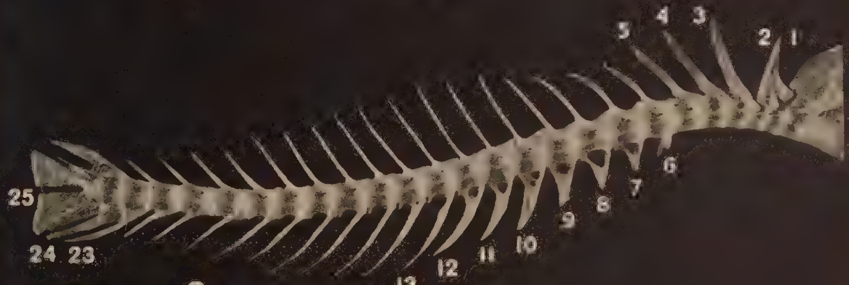


John Bale Sons & Curnow, Ltd London

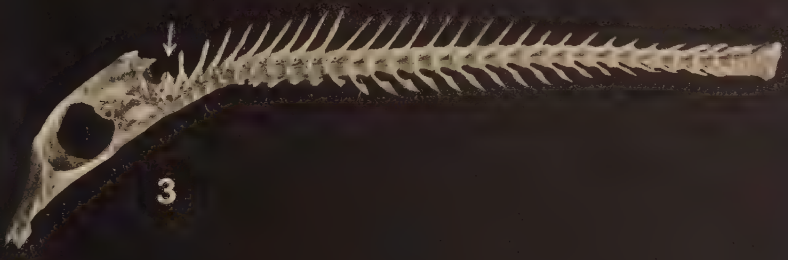
Figs. 1 and 2. Thick-lipped Grey Mullet. Fig. 3. Thin-lipped Grey Mullet.


7
6
5
4
3
2
1
31
30
29
8
9
10
11
12
13
14
15

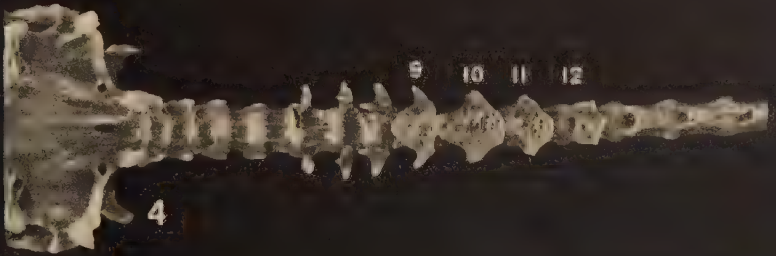
1


5
4
3
2
1
25
24
23
6
7
8
9
10
11
12
13

2



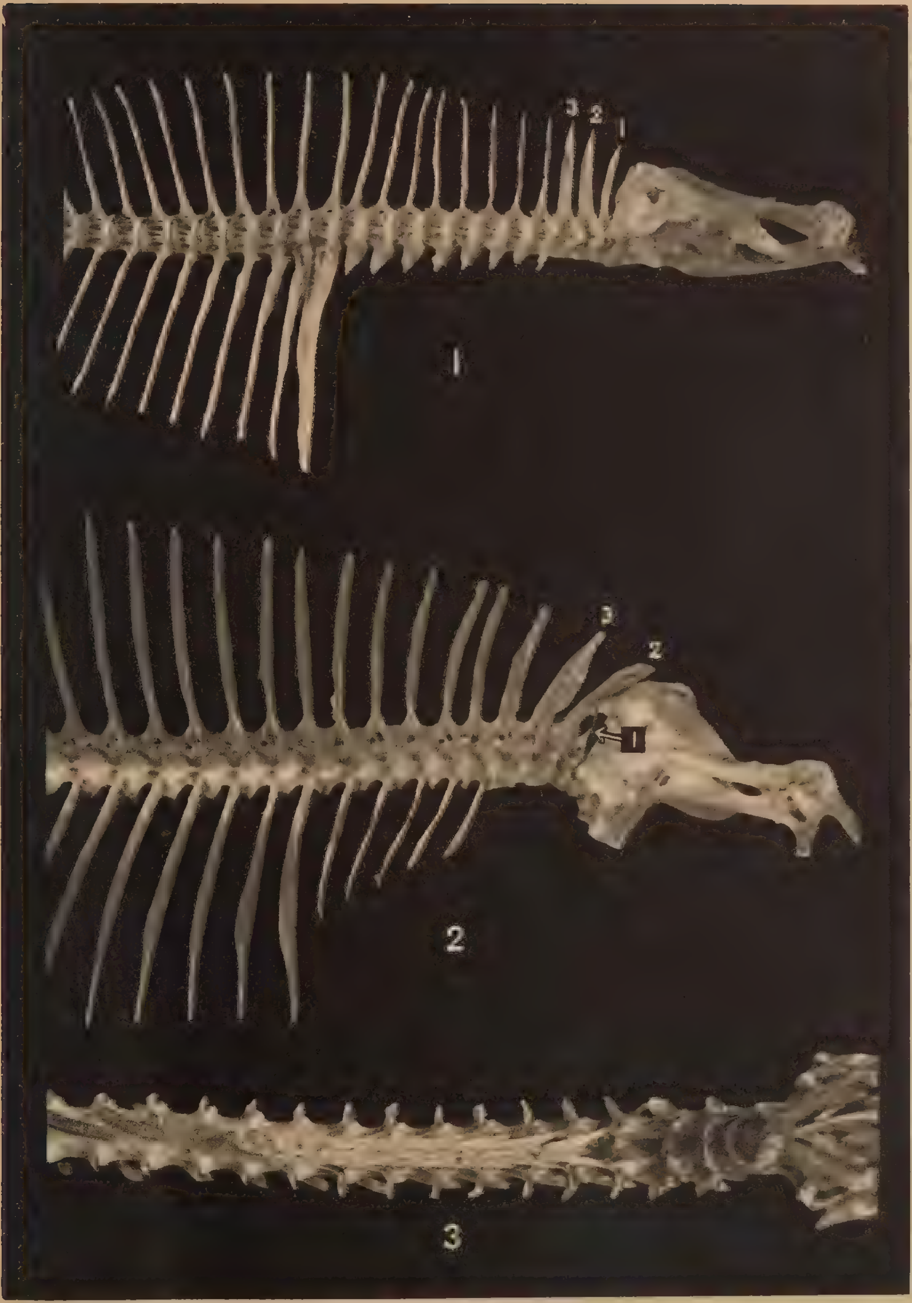
3



4

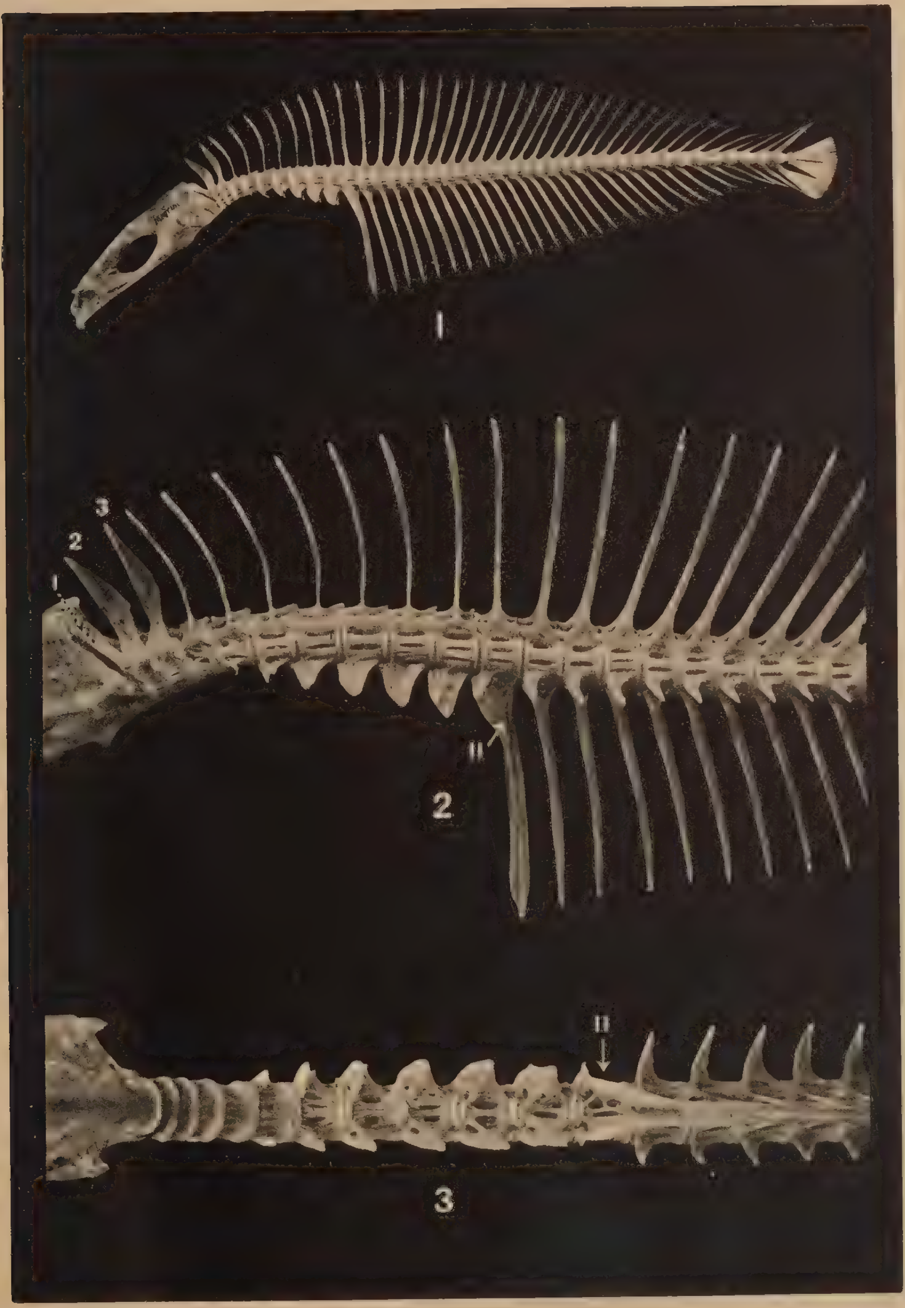
John Bale Sons & Curnow Ltd London

Fig. 1. *Sebastes marinus.* Fig. 2. *Scorpaena dactyloptera.* Figs. 3 and 4. *Trigla lyra.*



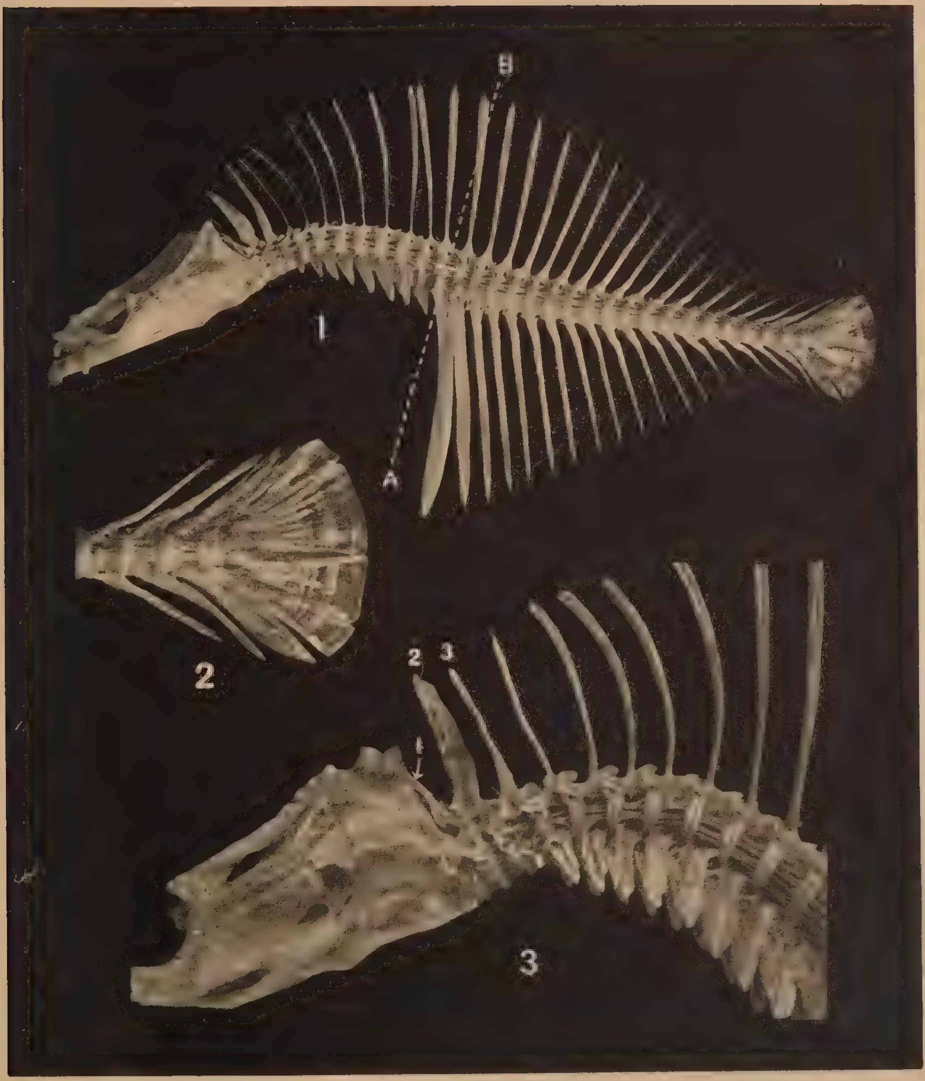
John Bale Sons & Curnow, L^td London

Fig. 1. *Pleuronectes flesus.* Figs. 2 and 3. *Solea solea.*


1
3
2
1
2
II
2
II
3

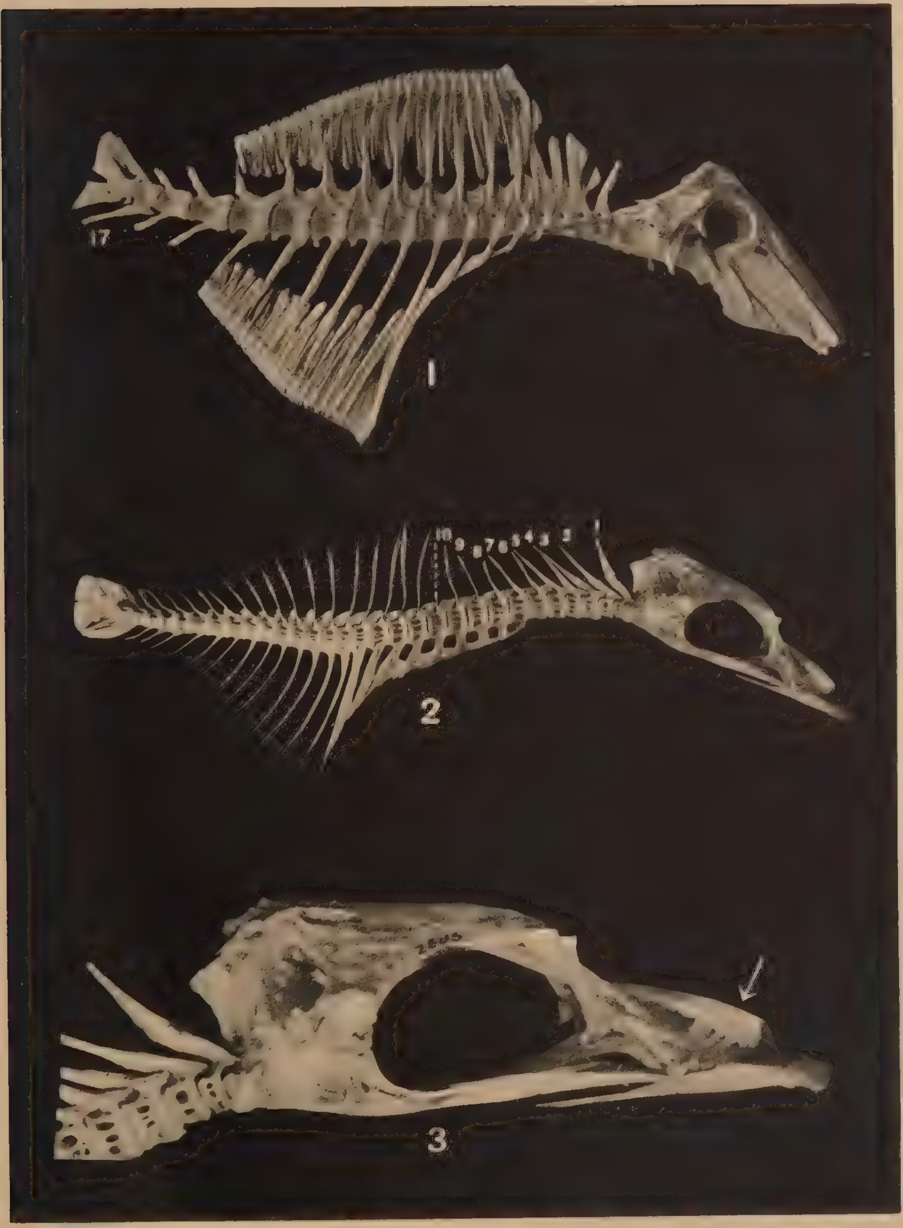
John Bale Sons & Curnow, L^td London

Figs. 1, 2 and 3. *Lepidorhombus whiff-iagonis.*



John Bale, Sons & Curnow, Ltd London

Figs. 1, 2 and 3. *Rhombus maximus.*


17
1
10
9
8
7
6
5
4
3
2
1
2
ZEUS
3

[illegible] London

Fig. 1. *Balistes capriscus.* Figs. 2 and 3. *Zeus faber.*

ON REARING THE HYDROIDS OF CERTAIN MEDUSAE, WITH AN ACCOUNT OF THE METHODS USED

By W. J. Rees, M.Sc.
Research Assistant at the Plymouth Laboratory
and F. S. Russell, B.A.
Naturalist at the Plymouth Laboratory

(Text-figs. 1–12)

The hydroids of the following four species of medusae have been successfully reared in the Plymouth Laboratory, *Amphinema dinema* (Péron & Lesueur), *Amphinema rugosum* (Mayer), *Rathkea octopunctata* (M. Sars) and *Mitrocomella brownei* (Kramp). It was not known previously which were the hydroids of these medusae.

Before giving an account of this work it is necessary to clear up some confusion that has arisen as to the identity of the two species of *Amphinema*. Two species occur at Plymouth, *A. dinema* (Pér. & Les.) and *A. rugosum** (Mayer) (see *Plymouth Marine Fauna*, 1931, p. 81).

The essential differences between the two species lie in the structure of the gonads, the form of the protuberances on the umbrella margin, and in the colour. Hartlaub (1914) gave a good description of *A. rugosum*, but unfortunately he gave this under the name *A. dinema*. He was, however, aware of the fact that there might be two species.

In *A. dinema* the gonads are simple adradial plates, the marginal protuberances are mere thickenings of the edge of the umbrella, and the colour of the two tentacle bulbs is a vivid purplish violet while the stomach is usually bright green. In *A. rugosum* the adradial gonads are folded to form a series of processes pointing inwards towards the interradii, the marginal protuberances are actually tentaculae with a central core of single endodermal cells, and the colour of the tentacular bulbs† and stomach is bright yellowish brown.

Mayer (1910) describes the gonads of the European form of *A. dinema* as "transversely folded", but his figure of a specimen from Mousehole, Cornwall, shows them as simple. In order to make certain of the structure of these gonads transverse sections were cut. These showed the gonads as being simple plates on each of the eight adradial surfaces of the stomach (Fig. 1). Examination of living specimens showed that the eggs tend to be distributed round the periphery of the plates, leaving a narrow central area free of eggs. In the males the plates are continuous.

---

* Mr E. T. Browne informs us that he and Dr P. L. Kramp have both agreed that this species is *Stomotoca rugosa* of Mayer (1900). As the generic name *Amphinema* is neuter the specific name should be *rugosum*.

† In Mayer's original description (1900) the tentacle bulbs are brick red, and in 1910 he gives the colour of stomach and tentacle bulbs as brick red, often streaked with sooty brown. This refers to American medusae.

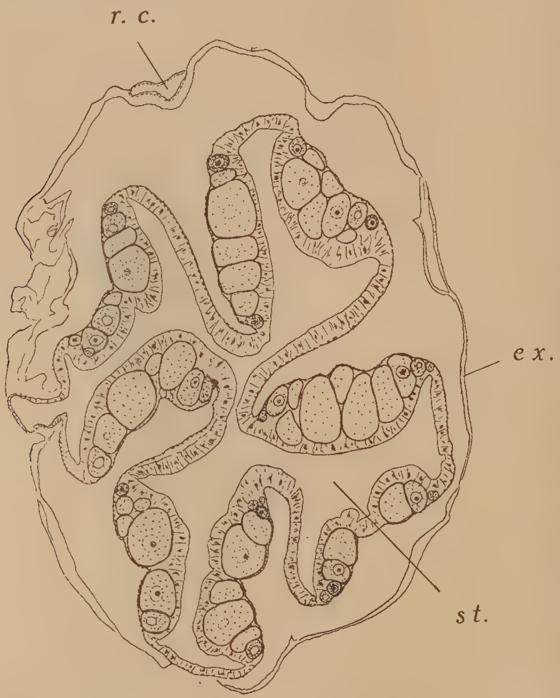


Fig. 1. Transverse section through stomach region of the medusa *Amphinema dinema*, showing disposition of ovaries on stomach. *ex.* exumbrella; *st.* stomach cavity; *r.c.* radial canal. (Del. F.S.R.)

Amphinema dinema (Péron & Lesueur)

The development of the egg to the first polyp has been described in detail by Rittenhouse (1910, as *Stomotoca apicata*) from medusae collected at Beaufort, North Carolina.

In October 1935 ripe *Amphinema dinema* medusae collected off Plymouth were isolated in a finger bowl and fertilized eggs obtained. Development proceeded as described by Rittenhouse. Medusae placed in bowls at 9.30 a.m. on October 10 had shed no eggs at 5.10 p.m., but at 9 a.m. the next morning eggs were present, mostly in the first cleavage stage. The eggs were opaque and 0·15 mm. in diameter. In the later stages of segmentation the blastomeres often became irregularly disposed. The planulae, which were 0·25 mm. long

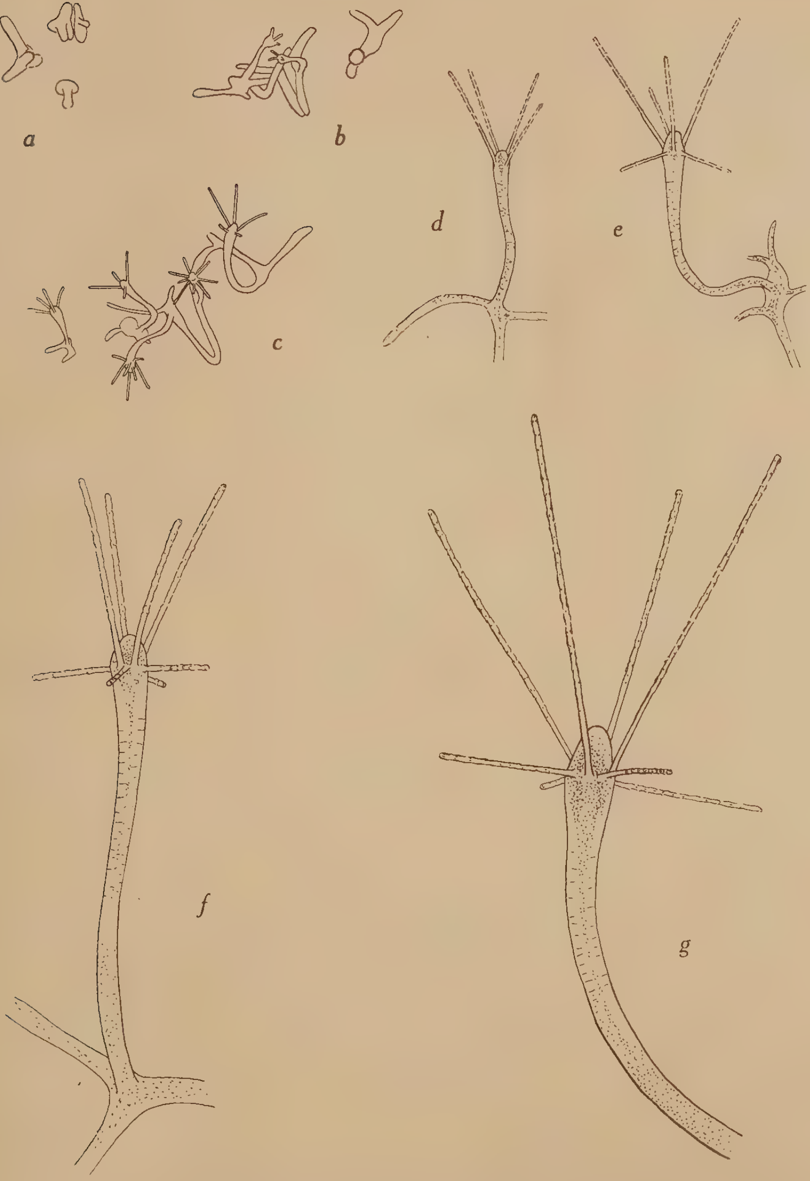


Fig. 2. *a–f*, stages in development of hydroids reared from *Amphinema dinema*. *a*, 9.45 a.m., 14. x. 35; *b*, 9.30 a.m., 15. x. 35; *c*, 11.15 a.m., 16. x. 35; *g*, Polyp of *Perigonimus serpens* dredged from Eddystone Grounds, 3. ii. 36. (Del. F.S.R.)

and 0·09 mm. wide, at first came to the surface but later settled to the bottom. The settled planula was pink and appeared to fix along its whole length, forming a stolon from the centre of which the first polyp developed (Fig. 2*a*). The development of the polyps was rapid, and 2 days after the settling of the planulae some had six tentacles. They were now a pale pink in colour. The young hydroids were kept until many had eight tentacles (Figs. 2*b–f*).

On February 3 1936 a colony of *Perigonimus serpens* was dredged from the Eddystone grounds attached to the base of a stem of *Eunicella verrucosa*. Except for their brilliant reddish orange coloration these polyps were identical in appearance with those reared from *Amphinema dinema* (Fig. 2*g*).

On March 20 and subsequent days a few medusae were liberated from this *Perigonimus serpens* colony. The young medusae (Fig. 3) were 0·6–0·7 mm. in height, the umbrella was slightly higher than wide, and there were scattered nematocysts on the exumbrella. There was no apical projection. The velum was broad. The stomach was cylindrical and about one-third the length of the subumbrella cavity. The mouth was simple. The four radial canals were fairly broad. There were two opposite perradial tentacles with large basal bulbs, two small opposite perradial marginal protuberances, and four indications of interradial protuberances. The colour of the tentacle bulbs and stomach was reddish orange, and in some there was a faint green tinge in the stomach.

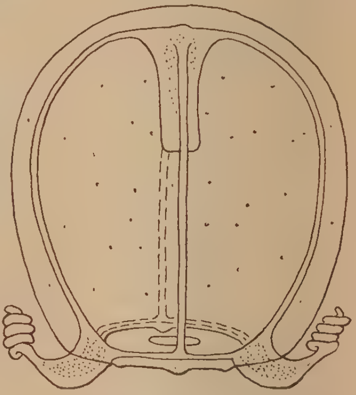


Fig. 3. Newly liberated medusa of *Amphinema dinema*, 0·7 mm. high, Plymouth, 21. iii. 36. (Del. F.S.R.)

The medusae were kept alive for several days but soon developed abnormally or turned inside out and died. The stomach in all specimens, however, turned a vivid green.

On October 14 1936 a further supply of mature *Amphinema dinema* medusae was obtained off Plymouth. After 3 days these medusae had shed a large number of opaque eggs 0·14–0·155 mm. in diameter. These were separated into three finger bowls. By October 21 planulae had developed in all three bowls; they were yellowish white or slightly pinkish in colour. They were ciliated all over, and the anterior end was blunter and thicker than the more pointed posterior end. They were 0·25 mm. in length and 0·085–0·09 mm. in width. The planulae attached themselves to the glass along their whole length to form short stolons from the centre of which the young polyps developed. New stolons also grew out from their sides so that by October 24 when the first polyps had developed the presence of three radiating stolons was a characteristic feature (Fig. 2*f*). The hydranths were club-shaped with four to six tentacles. Both polyp and hydrocaulus were somewhat brownish in colour. Two days later a piece of glass carrying the young hydroids was cut from the bowl and hung in a beaker in which the water was kept agitated. The polyps now fed on small copepods and nauplii, and their stolons soon began to ramify over the glass and send up secondary polyps. These gradually became pale orange brown in colour.

Polyps reared in the other two finger bowls were not removed to beakers until October 30, but although fed and kept under the same conditions as the first colony transferred they did not thrive. They lived for many months (until March 1937) but never appeared healthy, a condition possibly brought about by starvation in the finger bowls at a critical stage of their development.

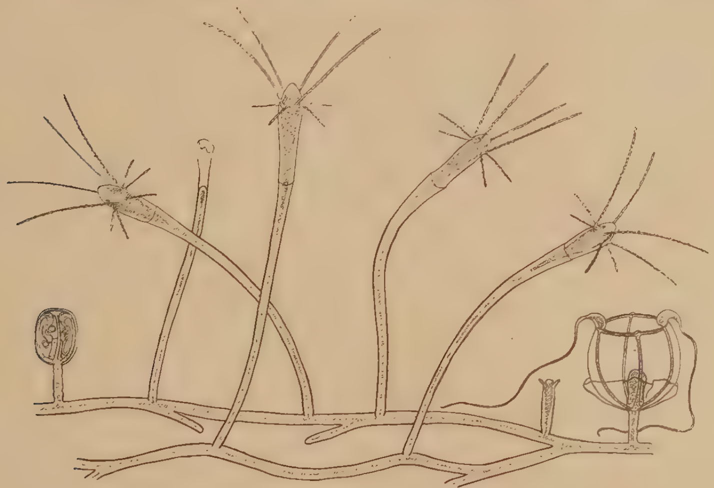


Fig. 4. Colony of hydroid with medusa buds reared from the medusa *Amphinema dinema* in the laboratory, Plymouth, 21. xii. 37. (Del. W.J.R.)

The initial polyps when fully grown (Fig. 4) were club-shaped and had eight filiform tentacles in a single whorl round the bluntly conical hypostome. The secondarily developed polyps were similar in form, each with a whorl of six to ten, usually eight to ten, alternately elevated and depressed tentacles. There was no sharp demarcation between the hydranth and the hydrocaulus. The limits and relative thickness of the perisarc of the hydrocaulus were clearly shown by staining with chlorazol black (see Cannon, 1937). In young polyps the perisarc is very difficult to see; in older specimens it is thin, non-annulated and transparent and adheres closely to the coenosarc, becoming horn coloured in the oldest parts.* At its point of origin from the stolon it may occasionally be slightly wrinkled. At its upper end it becomes very thin and membranous and does not form a true cup round the base of the hydranth. In well-grown specimens, however, it may enlarge to form a simple narrow funnel which is very elastic and bends with the hydranth, fitting it like a glove. The membranous portion of the perisarc is almost invisible in living specimens, but when the polyp dies down it can be clearly seen before it eventually breaks off. The upper limits of the perisarc could however sometimes be seen in starved polyps in which the neck of the hydranth had shrunk and become narrower than the region below to which the surrounding perisarc was adhering. The figure given by Hincks (1868, pl. 16, fig. 3) has this appearance.

---

* On November 12 1907, Mr E. T. Browne recorded a specimen dredged from the Duke Rock on a Laminaria root (see *Plymouth Marine Fauna*, 1931, p. 67). His manuscript notes say that some of the polyps were "clothed with particles of fine mud, etc." From the description in his notes there can be no doubt that he had the *A. dinema* hydroid.

As the colony grew older the creeping stolons anastomosed to form an open network; the colour of the polyps deepened to a bright reddish orange, the tip of the proboscis remaining white. By the end of November the colony was very large and healthy and covered all the available surface of the glass. The hydrocaulus occasionally branched once.

On December 14 medusa buds were developing, rising from the creeping stolons on short stalks (Fig. 4). The stalk was somewhat wrinkled and was never longer than the fully grown medusa bud. Buds nearly ready for liberation were 0·30–0·33 mm. long and 0·20–0·23 mm. wide, with stalks 0·20–0·22 mm. in length and 0·05 mm. in width. When the bud reached its full size the thin enclosing membrane ruptured and its remains could be seen attached to the top of the stalk. The two long tentacles were uncoiled in the water, and after many pulsations the bell broke away from the peduncle. The newly liberated medusa was identical in every respect with that described above from *Perigonimus serpens*, its height being also 0·7 mm.

On March 4 and May 26 1937 two colonies of *P. serpens* attached to pieces of dead *Eunicella* were dredged off the Mewstone. These colonies and the living colony reared from *Amphinema dinema* were compared side by side. In form and colour they appeared identical. The following measurements (in mm.) made on one of the colonies revealed no appreciable differences in dimensions.

	Perigonimus serpens (dredged)	*Amphinema dinema* (reared from medusa)
Height of polyp	1·2 –2·5	1·5 –2·3
Diameter of hydranth	0·12–0·14	0·11–0·15
Diameter of hydrocaulus	0·05–0·10	0·05–0·08
Length of longer tentacles expanded	0·5 –0·7	0·7 –1·1
Length of shorter tentacles	0·25–0·4	0·35–0·5

In both colonies the number of tentacles on a single hydranth was rarely less than eight or more than ten. One of these colonies produced medusae identical with those described above. There can therefore be no doubt that the hydroid reared from the medusa *Amphinema dinema* (Pér. & Les.) is identical with *Perigonimus serpens* Allman.

Amphinema rugosum (Mayer)

A hydroid colony of the *Perigonimus serpens* type, bearing medusa buds, was found on a floating piece of cork off Drake's Island on May 25 1937. The colony had a much more robust habit than *P. serpens*, the hydroid of *Amphinema dinema*, and the structure of the liberated medusae on the next day confirmed the view that the species was distinct from *A. dinema*. A detailed examination of the trophosome revealed differences which appear to be specific.

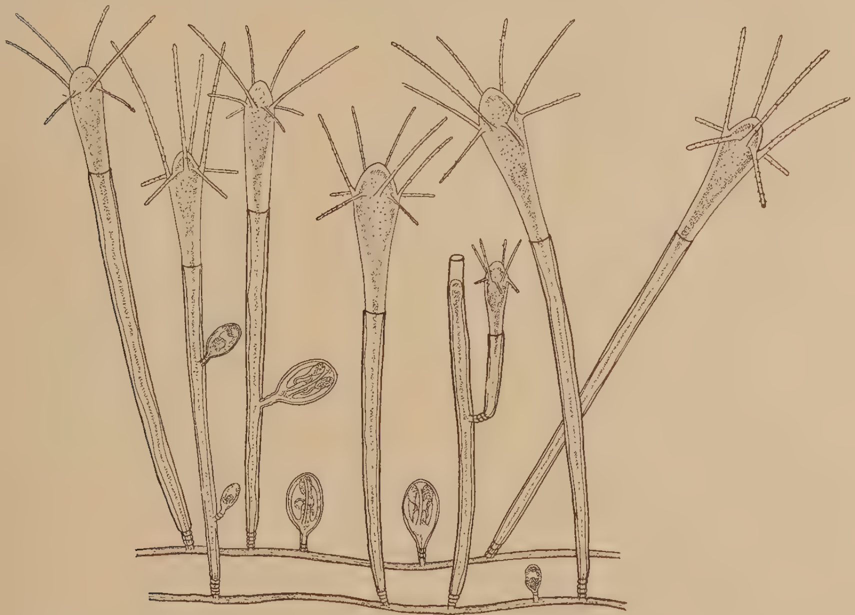


Fig. 5. Colony of hydroid of *Amphinema rugosum*, Plymouth, 25. vi. 37. (Del. W.J.R.)

The hydranths and coenosarc possessed the same bright reddish orange colour so typical of *Perigonimus serpens*, but the polyps were distinctly larger and the hydrocauli were firmer and longer, growing close together as upright tufts (Fig. 5). The stems rose to a total height of 2·5–3·5 mm. from the substratum. The stolons were creeping and branched, 0·05–0·06 mm. in diameter. Both hydrocauli and stolons have a firm horn-coloured perisarc. The perisarc is annulated just above the origins of the stems, the annulations varying in number from two to five. At their point of origin the stems have the same diameter as the stolons, but above the annulations they become much thicker with a diameter of 0·10–0·15 mm. The hydrocaulus sometimes branched once or twice, the branches being always annulated at their point of origin.

The perisarc at the top of the hydrocaulus reached a diameter of as much as 0·2 mm. in old polyps, but the enlargement towards the upper end was more gradual and less demarcated than in the hydroid of *Amphinema dinema* and the upper end was not membranous. The perisarc always ended abruptly and the hydranth was not at all retractile. That part of the stem covered by perisarc was 2·0–3·0 mm. long.

The hydranths were large and club-shaped, 0·5–0·75 mm. in length, and had eight to twelve filiform tentacles, alternately elevated and depressed, around a conical hypostome. The tip of the hypostome was opaque white, the rest of the hydranth being bright reddish orange. The nematocysts were scattered along the tentacles as in the *A. dinema* hydroid.

The medusa buds were borne on short stalks 0·15–0·22 mm. long both on the stolons and on the hydrocauli. These stalks were wrinkled or annulated. The majority of the medusa buds arose from the stolon, and of the few that arose from the hydrocauli there were never more than two on each hydrocaulus. The largest buds were 0·35 by 0·25 mm. The medusa buds were covered by a thin perisarc which ruptured to liberate the medusae.

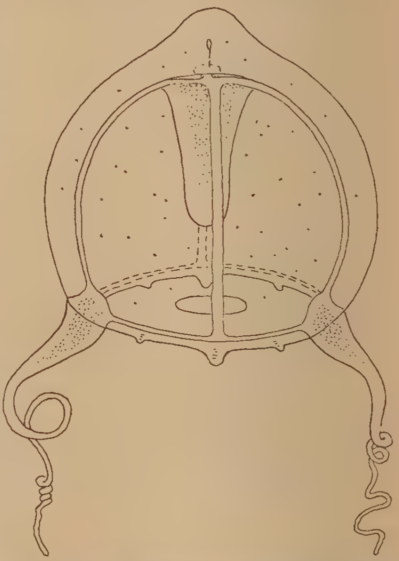


Fig. 6. Newly liberated medusa of *Amphinema rugosum*, 0·55 mm. high, Plymouth, 26. vi. 37. (Del. F.S.R.)

The newly liberated medusae were 0·42–0·65 mm. in height (Fig. 6). The umbrella was as wide as it was high; there were scattered nematocysts on the exumbrella. There was always a small apical projection and usually the remains of an apical canal. The velum was broad. The stomach was large and cylindrical and about half the length of the subumbrella cavity; it had a rather broad base. The mouth was simple. The four radial canals were fairly broad. There were two opposite perradial tentacles with large basal bulbs; two small opposite perradial young marginal tentaculae and four interradial tentaculae developing, in all of which an endodermal core was present. The colour of the tentacle bulbs was reddish orange, with a faint tinge of yellow along the under side; the colour of the stomach was bright ochreish yellow with traces of the tentacular reddish orange pigment at its base.

This medusa thus differed from the first stage of *A. dinema* in the following points; it possessed an apical projection; the perradial and interradial marginal protuberances were much more pronounced and obviously developing tentaculae; the colour of the stomach was quite distinctive—typical of that of the adult *A. rugosum*. Although kept alive for several days there was no sign of green coloration on the stomach. There can be little doubt that these were *A. rugosum*.

The characteristics of the hydroid described above were confirmed from a microscopical preparation kindly sent by Mr E. T. Browne of a specimen that he obtained on October 8 1897.* His manuscript notes read as follows:

> *Perigonimus ?serpens.*
>
> On a crab-pot rope. About 3 miles south of Mewstone. A small *Perigonimus* which corresponds somewhat to the description given by Allman of *P. serpens* is very abundant upon the rope. It has gonophores upon the stolon and some free medusae were taken in the jar in which the colony was placed. The stolons (?) are often turned up and form stems upon which the gonophores are attached.
>
> 1898. Microscopical preparations of the colonies show that this hydroid does not correspond to the description of the *P. serpens* Allman. But it is more like *P. serpens* than any of the other species. There is no cup-like expansion of the perisarc at the base of the hydranth. The hydranths correspond to the figure given by Allman.
>
> Allman only figures the gonophores (medusae) upon the stolon. In the Plymouth specimens the gonophores are upon the creeping stolons and also upon the stems. The stems which bear the gonophores usually terminate in a large club-shaped knob. As a rule the fully developed hydranth has no gonophores attached to it, but occasionally an individual is seen with a gonophore on the stalk. The stems which bear gonophores also have hydranths, one or two, on short stalks and small in size.
>
> The stalk of the gonophore is slightly wrinkled as figured by Allman. The perisarc of the hydranth upon the stem is annulated like the gonophores.
>
> Hydranths with about ten to twelve tentacles.

A re-examination of this preparation has revealed no important differences from the hydroid of *Amphinema rugosum* described above. The dimensions of Mr Browne's specimen agree with ours and there can be little doubt that they are the same species. The essential differences between the two species are thus as follows:

	Amphinema dinema	*Amphinema rugosum*
Hydroid:		
Base of hydrocaulus	Not annulated	Annulated
Upper end of hydrocaulus	A membranous dilatation	Not membranous
Height of hydranth	1·5–2·3 mm.	2·5–3·5 mm.
Diameter of hydrocaulus	0·05–0·10 mm.	0·10–0·20 mm.
Medusa buds borne on	Stolon	Stolon and hydrocaulus
Medusa on liberation:		
Apical projection	Absent	Present
Colour of stomach	Reddish orange becoming green	Ochreish yellow

Perigonimus serpens was originally described by Allman (1863) from a colony found growing on the basal portion of *Plumularia setacea* in Torbay. From his description of the medusa liberated from the hydroid it is evident that Allman had the hydroid of *Amphinema dinema*. The medusa had no apical process and the marginal protuberances were not indicated as being so well developed as they are in the newly liberated medusa of *A. rugosum*. There were also no annulations on the hydrocaulus of the hydroid. The hydroid *Perigonimus serpens* has been recorded as follows: Torbay (Allman, 1872), Ilfracombe and Filey Brigg (Hincks, 1868), Plymouth (Marine Biological Association, 1931); North Sea (Winther, 1880; Hartlaub, 1897); Mediterranean (Richiardi, 1880; Motz-Kossowska, 1905, on *Cellaria fistulosa* and *Gorgonia* sp.). In view of the similarity between the hydroids of *Amphinema dinema* and *A. rugosum* it is, however, impossible to say for certain to which species these records refer.

---

* See *Plymouth Marine Fauna*, 1931, p. 67, recorded as *Perigonimus serpens*.

Allman (1863) referred his *Perigonimus serpens* to the genus *Perigonimus* Sars 1846 of which *P. muscoides* is the genotype. Stechow (1923) has suggested restricting the genus *Perigonimus* to *P. muscoides* and its nearest related forms and excluded provisionally all other so-called "*Perigonimus*" spp., which lack polysiphony and liberate medusae with two tentacles, on the grounds that they are not cogeneric with the genotype. For the moment he suggests placing all these species in the medusa genus *Leuckartiara* Hartlaub, 1914, presumably (although he does not say so) with *Perigonimus repens* Wright, 1857, as the genotype. Whether this step is justifiable with regard to all so-called "*Perigonimus*" spp. is uncertain because the adult stage of the gonosome of *P. muscoides* is not yet known and with few exceptions the medusae of all other "*Perigonimus*" spp. are also unknown. The medusa of *P. muscoides* is known however to be liberated with four tentacles already developed; it cannot therefore be cogeneric with the *P. serpens*-like hydroids of *Amphinema dinema* and *A. rugosum* in which the adult medusa never has more than two tentacles. For this last reason also *Amphinema* cannot be included in the genus *Leuckartiara*. It is therefore proposed to place these two hydroids provisionally in the medusa genus *Amphinema** Haeckel, 1879. The specific name "*dinema* Péron & Lesueur, 1809" has priority over Allman's *Perigonimus serpens* which he used to describe both the hydroid and young medusa. *P. serpens* Allman thus becomes synonymous with *Amphinema dinema* (Pér. & Les.), while the other hydroid here described for certain for the first time* becomes *A. rugosum* (Mayer).

---

* Haeckel (1879) established the genus *Amphinema* for "Tiarids with two opposite perradial tentacles. No peduncle. No mesenteries. Stomach with broad base. Gonads four pairs of adradial longitudinal swellings with cross-folds or four perradial pinnate plates (gefiederte Blätter)." Hartlaub (1914) redefined the genus as having "Gonads forming adradial series of pockets". The genus should now be redefined as "Pandeids with two opposite perradial tentacles. No peduncle. No mesenteries. Stomach with broad base and not extending beyond umbrella margin. Gonads four pairs of adradial simple or folded swellings. Hydroid '*Perigonimus serpens*'-like."

Some authors have regarded *Amphinema* as synonymous with *Stomotoca* Agassiz, 1862, the species of which have a peduncle. Whether this should be regarded as a specific character must be a matter of opinion, but until the hydroids of the species of *Stomotoca* are known it is advisable to keep the two genera separate. If, however, the hydroid should be found to resemble those of the *Amphinema* species here described the name *Amphinema* may have to give way to *Stomotoca*. A full discussion of the synonymy of the group seems premature until more is known about the hydroids.

Haeckel called his genotype *Amphinema titania*. This was the specific name given by Gosse (1853, p. 387, pl. XXVI, figs. 7–9) to what was presumably *A. dinema*. Unfortunately, Haeckel has described the medusa as having folded gonads and his figures (pl. IV, figs. 8 and 9) resemble much more closely *A. rugosum*. There seems little doubt that he has confused the two species. In our new definition of the genus *Amphinema* we regard *A. dinema* (Pér. & Les.) as the genotype.

While discussing *Perigonimus* spp. it seems opportune to bring forward the question of the identity of a species described by Hincks (1877) as *P.*? *nutans*. From the description and figure of this hydroid it seems very possible that it was a young polyp of the *P. serpens* type. There will never be any possibility of the certain identity of the species, and as it possesses no annulations at the base of the hydrocaulus we propose that the name *P.*? *nutans* Hincks should be sunk in the synonymy of *Amphinema dinema*.

Rathkea octopunctata (M. Sars)

A number of mature medusae of *Rathkea octopunctata* were caught off Plymouth in April 1937. The first successful fertilizations were obtained on April 14. The eggs were opaque white, and 0·14 mm. in diameter. Planulae had developed on the 18th; these were ciliated and pear-shaped, being 0·15 by 0·1 mm. These planulae, some of which were kept in the dark and some in the light, failed to settle on the glass bottoms of the bowls.

Another successful fertilization was made on April 20, and 3 days later planulae had developed from eggs 0·14 mm. in diameter. These were distinctly larger and more active than those previously mentioned; they were 0·20–0·24 mm. in length and 0·08–0·09 mm. in width. In shape they were somewhat cylindrical and bluntly rounded at both ends, the anterior end being usually slightly the wider. Some planulae about to settle had a slight depression at the posterior end.

A small piece of skeleton from the basal stem of *Eunicella verrucosa* (which had been previously boiled) was placed in a bowl with planulae in it on May 1. The next day at 3.30 p.m. about six planulae had settled on the *Eunicella* and others were in the act of settling. They attached by the anterior end leaving the posterior end free. On May 5 tentacles were developing at the free end of the larva, and on the next day a few had three or four very short tentacles. The maximum height of the polyps at this stage, including the tentacles, was 0·20 mm.

By May 7 the tentacles had grown in size and were capable of considerable extension, becoming very delicate and thread-like when fully extended as in *Trichydra*. They were arranged in a single whorl of three or four around a slightly opaque white proboscis. On the same date a single polyp with three tentacles was found attached to the glass bottom of another bowl. While searching in this bowl it was suddenly found that there were great numbers of extremely fine tentacular processes issuing from two small masses of detrital matter stuck to the glass. These proved to belong to polyps which must have developed from planulae which had found here a peculiarly suitable settling ground. Other bowls, which had been set on one side since there were no signs of settled planulae on the glass, were then examined, and several more very small masses of detritus were found each with large numbers of fine tentacles issuing from them. In these, of course, the developing planulae would have been completely buried and invisible. These polyps were exactly the same in every respect to those which had developed on the *Eunicella* from planulae which were seen to settle. There can thus be no possibility that the polyps or planulae from which they arose had been carried into the bowl with the outside sea water used. Rather it was that the small amount of detrital matter which is always present in unfiltered sea water had collected together on the bottom to form small flocculent masses of just the right texture for the Rathkea planulae to settle in, and these had cemented the detritus to the glass. Measurements of one of these polyps on May 7 showed the hydranth projecting out of the detritus only to a length of 0·1 mm., the extended tentacles measuring up to *ca.* 0·4 mm. in length.

---

* Brooks (1883) described from Beaufort, North Carolina, a hydroid from which he reared "*Amphinema apicatum* (Haeckel)". The synonyms he gave are those of the American form of *A. dinema*. Mayer (1910) has, however, regarded Brooks' hydroid as being that of *A. rugosum*. Brooks' description of the young medusa fits closely to *A. dinema*; there was no apical projection in the first stage and only marginal enlargements rather than tentaculae are mentioned. His description of the hydroid differs from *Perigonimus serpens* in that the medusa buds arose from the stems; in fact Brooks likened the hydroid to *P. minutus*.

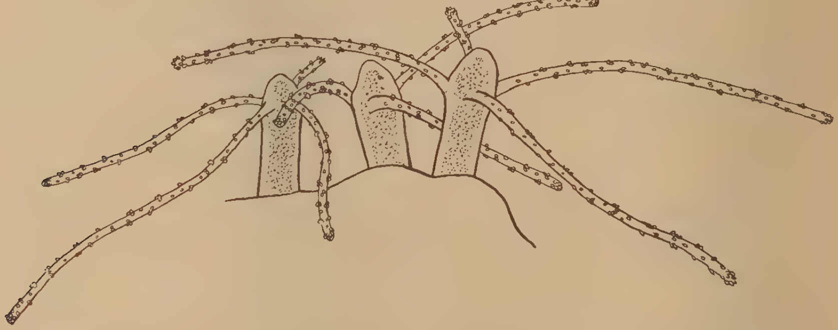


Fig. 7. Hydroids reared from the medusa *Rathkea octopunctata* attached to a piece of stem of *Eunicella*; tentacles partially contracted, Plymouth, 15. v. 37. (Del. W.J.R.)

On May 10 a large number of polyps were found on the *Eunicella* which were not previously visible. The planulae of these had settled in the deep crevices and depressions of the broken ends of the stem, and it was only when their tentacles were extended that they became visible.

Polyps which had developed on the smooth sides of the *Eunicella* stem (Fig. 7) by May 28* (i.e. about 1 month old) still measured only about 0·15–0·20 mm. in height from the substratum to the top of the hypostome, while those in the detrital masses were extended to a length of 0·12–0·27 mm. There were usually four or five tentacles, and occasionally six, in a single whorl. The tentacles were capable of great extension, to a length of 1·3 mm., and when fully extended were extremely delicate and thread-like. If the water was disturbed while the tentacles were fully expanded they were thrown into loose uncontrolled curves. When seriously disturbed, however, they could contract so that they reached only a short distance above the end of the hypostome.

---

* After 5 months (28. ix. 37) some polyps are still alive and show no further development.

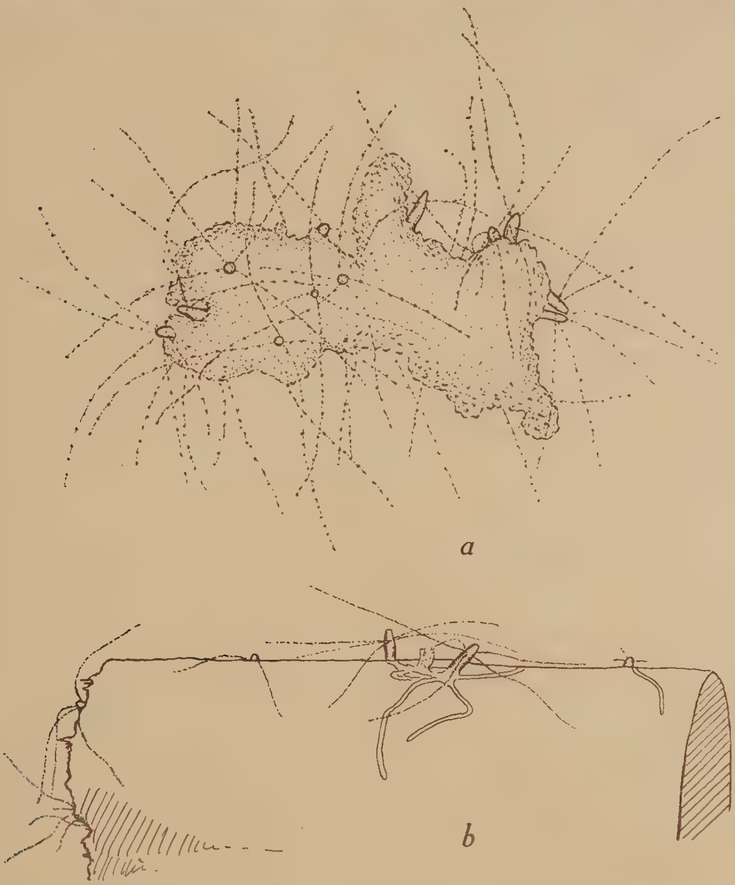


Fig. 8. *a*, colony of hydroids reared from the medusa *Rathkea octopunctata* whose planulae settled in a small mass of detritus, Plymouth, 28. v. 37. (Del. W.J.R.) *b*, hydroids reared from *Rathkea octopunctata*, Plymouth, 28. v. 37, drawn to show stolons creeping over stem of *Eunicella* and typical attitude of the tentacles of the polyps. On the right is a developing secondary polyp. Between the two centre polyps is an empty perisarc tube. Tentacles are also seen on the left side issuing from polyps growing in clefts at the broken end of the stem. (Del. F.S.R.)

The tentacles when extended are held out at right-angles so that they lie absolutely flat along the surface of the substratum (Fig. 8*b*). In polyps in the detritus which were perforce projecting out horizontally, those tentacles on the lower side were pressed firmly against the glass. A detrital mass left under the microscope some time to allow the polyps to expand fully had a pin-cushion-like appearance with the tentacles projecting in all directions (Fig. 8*a*).

The tentacles had a core of single cylindrical endoderm cells and were covered with large numbers of nematocysts arranged in somewhat irregularly scattered groups. When the tentacles were contracted these nematocysts had the appearance of being arranged in whorls. The nematocysts measured 0·005–0·007 by 0·002–0·003 mm.

The hydranth body was cylindrical in form and had an elongated hypostome about 0·05–0·08 mm. in length. This hypostome was opaque white, the rest of the polyp being colourless. The lower part of the body of the hydranth was apparently surrounded by a very thin gelatinous perisarc which was very difficult to see. Its presence was, however, indicated by detrital matter which adhered to it very easily. In fact the whole mass of detritus seemed to be held very firmly together by its adherence to the numerous perisarc tubes, and it was almost impossible to dissect a single polyp away intact.

These observations probably indicate the normal habitat of the hydroid and explain why it has not been discovered in the field. The hydroid probably lives on stones covered with a felt of minute algae and detrital matter, with only the hypostome projecting above the detrital layer and the tentacles lying flat over the surface of this layer ready to catch any minute creeping organisms. They may also live in little clefts on rough material with only their tentacles projecting.

It seems quite impossible to identify this hydroid certainly with any known described species. It appears to resemble *Eudendrium pudicum* of Van Beneden (1866), and also perhaps *Perigonimus* (?) *quadritentaculatus* of Hincks (1868), though it differs from the latter in that all its tentacles are of equal length. The great elongation of the tentacles and their delicate thread-like character is comparable with that of *Trichydra pudica* Wright. The *Rathkea* hydroid, however, lacks the distinct collar-like hydrothecal perisarc, and its hydranth body is not capable of the great extension so typical of *Trichydra*. The manner of holding the tentacles is also different.

It seems to us, therefore, wiser on the whole that any attempt to identify this hydroid should be given up and that for the time being it should bear the name of its medusa *Rathkea octopunctata*.

One thing is certain. The hydroid is not a *Bougainvillia*, and *Rathkea* can therefore be removed once and for all from the Margelidae and possibly placed in a family of its own.

Mitrocomella brownei (Kramp)

At the end of April 1937 five mature specimens of *M. brownei* were obtained off Plymouth. While four of these were females fortunately one was a male and a successful fertilization was made. The structural details of the medusae used were as follows:

	Diameter mm.	Tentacles	Developing bulbs	Marginal vesicles
Female	5	14	2	11
,,	5	16	3	10
,,	6	16	6	10
,,	7	15	5	10
Male	5	11	5	11

The eggs were colourless and 0·095 mm. in diameter. They were apparently shed at night. For instance, a bowl in which the medusae had shed no eggs at 4.45 p.m. on May 7 had many gastrulae at 10 a.m. the next day; this was repeated with the same results on three successive occasions. The planulae were 0·16 mm. in length and 0·08 mm. wide, the anterior end being slightly the thicker. The gastrulae, which were oval, remained on the bottoms of the bowls; the next day, when they were developing into planulae by proliferation of endoderm in the anterior end of the cavity, they were swimming at the surface. On the following day the fully developed planulae were once more on the bottom and within 24 hr. they appeared to be seeking for settling spots. Planulae which had developed from eggs laid between the afternoon of May 5 and morning of May 6 had fixed to the glass by the morning of the 10th. The next day the perisarc was developing, and within 3 days the perfect hydrotheca was formed and the polyps had tentacles.

The hydroid (Figs. 9 and 10*a* and *b*) is a species of *Cuspidella*. The hydrothecae are 0·2–0·3 mm. in length and 0·05–0·06 mm. wide. The hydranth was very extensile and could extend beyond the operculum to a length of 0·5 mm., the tentacles being 0·16 mm. long. There were eight to twelve tentacles in a single whorl, alternately elevated and depressed.

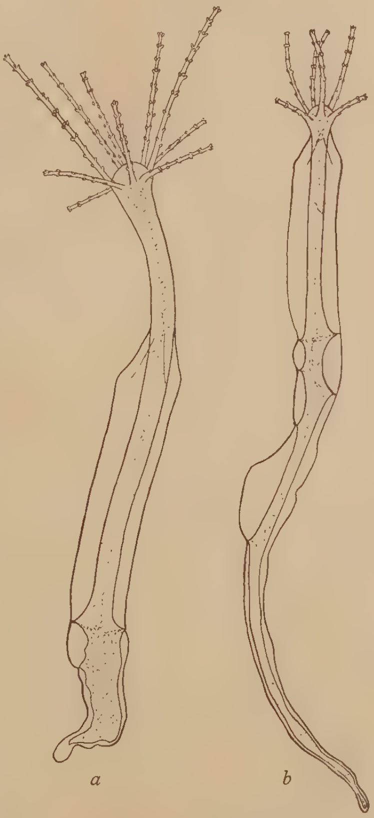


Fig. 9. Young stages of polyps reared from the medusa *Mitrocomella brownei*, Plymouth, 18. v. 37. Width of hydrotheca: *a*, 0·06 mm.; *b*, 0·05 mm. (Del. W.J.R.)

This *Cuspidella* is thus about half the size of that reared from *Laodicea undulata* (Russell, 1936). While *Cuspidella* of the *Laodicea* size is quite common off Plymouth we have at times seen a very small species corresponding in dimensions with that reared from *Mitrocomella brownei*. A drawing of such a hydroid is given in Fig. 11; it differs only in having fourteen tentacles which the *Mitrocomella* hydroid may well have when fully developed.

The question of the actual specific name of this hydroid must remain a matter of opinion. Hincks (1868) records three species, *Cuspidella costata*, *C. grandis*, and *C. humilis*. Unfortunately, he gave no measurements from which accurately to gauge their size. Stechow (1923, p. 133) has given measurements of *C. humilis* hydrothecae as 0·065 mm. wide. This almost agrees with the dimensions of the hydroid of *Mitrocomella brownei*, but in view of the fact that there may be other medusae with similar hydroids it seems to us safer to give the hydroid the name of the medusa.

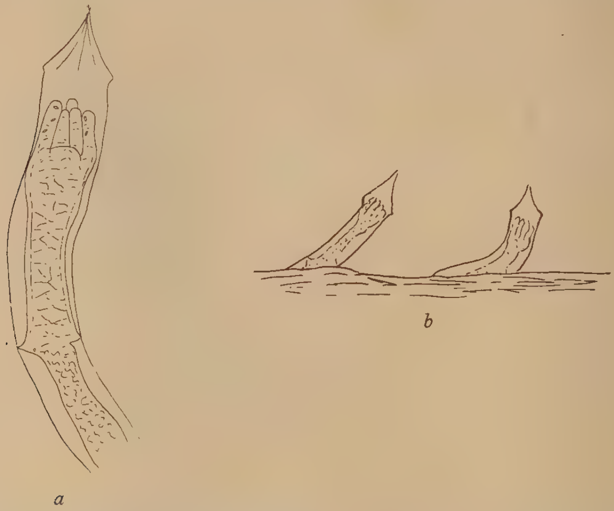


Fig. 10. *a*, polyp reared from *Mitrocomella brownei*, Plymouth, 15. v. 37. Width of hydrotheca 0·06 mm. *b*, polyps reared from *Mitrocomella brownei* attached to stem of *Eunicella*. (Del. F.S.R.)

While discussing *Mitrocomella* mention should be made of a further observation. The two genera *Mitrocomella* and *Cosmetira* are differentiated on the grounds that in the former the marginal cirri coil spirally while in the latter they do not (Kramp, 1932). We have examined living specimens of *Cosmetira pilosella* and can state definitely that the cirri can and do coil spirally. This is especially noticeable in the younger stages, but when the medusa is preserved they are nearly all straight. It is therefore questionable whether the genus *Mitrocomella* should be retained, and it seems better that it should be sunk in *Cosmetira*.

Browne (1910) kept *Cosmetira* and *Mitrocomella* distinct on the grounds that the former had only eight marginal vesicles while the latter had sixteen. This was before *M. brownei*, which normally has only eight vesicles (Kramp, 1932), had been described. It thus seems that this distinction also can no longer be held valid.

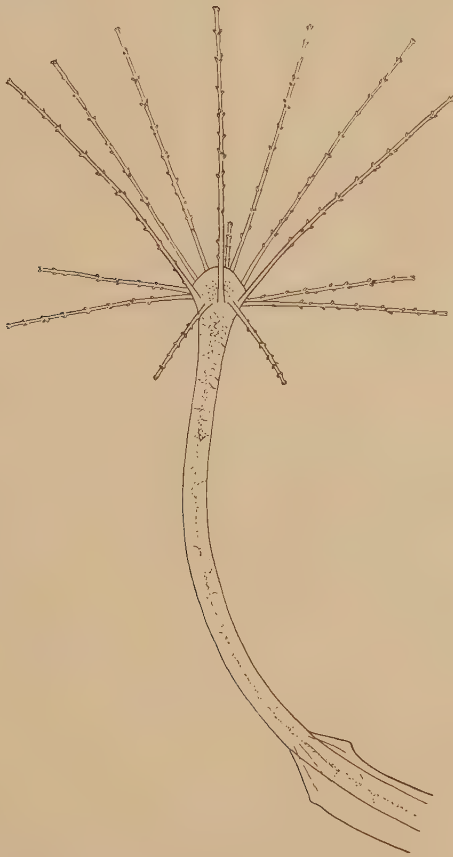


Fig. 11. Fully expanded polyp of *Cuspidella* dredged from the Cattewater, 30. i. 36. Width of hydrotheca 0·06 mm. (Del. F.S.R.)

THE METHODS OF REARING

During the past 50 years a number of British species of medusae have been linked to their respective hydroids. But the proportion whose hydroids remain unknown is still high. It is noticeable that most of those already linked are species whose hydroid colonies are very common, or large and easily found, and can thus often be obtained with medusa buds already developed. The remaining species are therefore likely to be found among the minute and less conspicuous forms. These are easily damaged while being caught and brought to the laboratory, and even if after much searching they are found the chances are slight that they will have medusa buds developed.

It was found that if small pieces of shell, stone or other objects recently dredged are left to stand for several days in bowls of outside sea water, polyps will regenerate from living stolons. In this way a number of the more minute species have been obtained. They must be kept alive until they produce medusae, and we have been able to keep colonies living for many months by the method to be described below. This method is, however, tedious, and the quickest and most certain method is to rear the hydroids from the eggs obtained from living medusae. Primary polyps have been reared from a number of species by the earlier workers, e.g. Metschnikoff, for embryological studies, but few of these were ever grown into colonies.

The method we are now using is to rear the first polyps in finger bowls from ripe medusae caught in numbers in the plankton. These are at first fed individually with small organisms such as copepod nauplii until other polyps have started growing. The glass or other object to which the small hydroids are attached is then removed and hung up by a silk thread in the apparatus described below.

The pioneer work of Browne (1898), who introduced the plunger jar system, showed that by keeping the water agitated the necessity for constant renewal of water could be obviated. Browne (1907) also described a method whereby food could be brought to a fixed hydroid colony by means of a constant current. One of the main practical disadvantages of these methods is that owing to the large volumes of water which are used much space is occupied in the laboratory and a long time is spent in searching for minute organisms.

Dr H. W. Harvey, while studying the growth of plankton diatoms, devised a method of preventing the diatoms from settling on the bottom. Its advantages were at once obvious for the rearing of hydroids and medusae, and we are much indebted to him for a method which has proved extremely successful for our research.

The essential principle is that a glass plate cut to a suitable size stands upright in a beaker so that it may be rocked backwards and forwards. Owing to the curvature at the bottom of the beaker the lower edge of the glass plate remains slightly above the bottom, leaving a clearance through which a current of water passes when the upper edge of the plate is rocked backwards and forwards. By using beakers the necessity for much space is eliminated, and we have been able to set up a battery of beakers on a small bench in which a large number of hydroids can be kept alive at the same time.

The beakers used are $5\frac{1}{2}$ in. in height with an internal diameter of 4 in. The glass plates are about $4\frac{3}{4}$ in. in length and cut just wide enough to fit the beaker without scraping its sides. The two bottom corners of a plate rest upon the incurved sides at the foot of the beaker and pivot there, while the upper edge of the plate has a backwards and forwards play of about 1 in. A glass rod, with a bent end, hooks over the top edge of the plate, the straight body of the rod projecting through the beaker spout. The free end of the glass rod is attached to a wire stretched between wooden uprights (Fig. 12*a*) by a rubber tube whose end is split, the two ends of this split are fastened with a pin after the wire has been inserted between. The wooden uprights are fixed to a long horizontal wooden batten (Fig. 12*b*) which is pivoted at either end in two angle irons screwed to the bench. A string attached to the wire which works the main plunger jar system (Fig. 12*P*) of the laboratory passes under a pulley on the bench to the top of a central wooden upright on the batten. The wooden structure is set so that in the forward position of the glass plates in the beakers it is leaning slightly backwards; on the release of the tension on the plunger string it then drops backwards about an inch under its own weight against a stopper (Fig. 12*c*). It is convenient to have two wires at slightly different levels on the wooden uprights to allow for inequalities in the heights of the beakers.

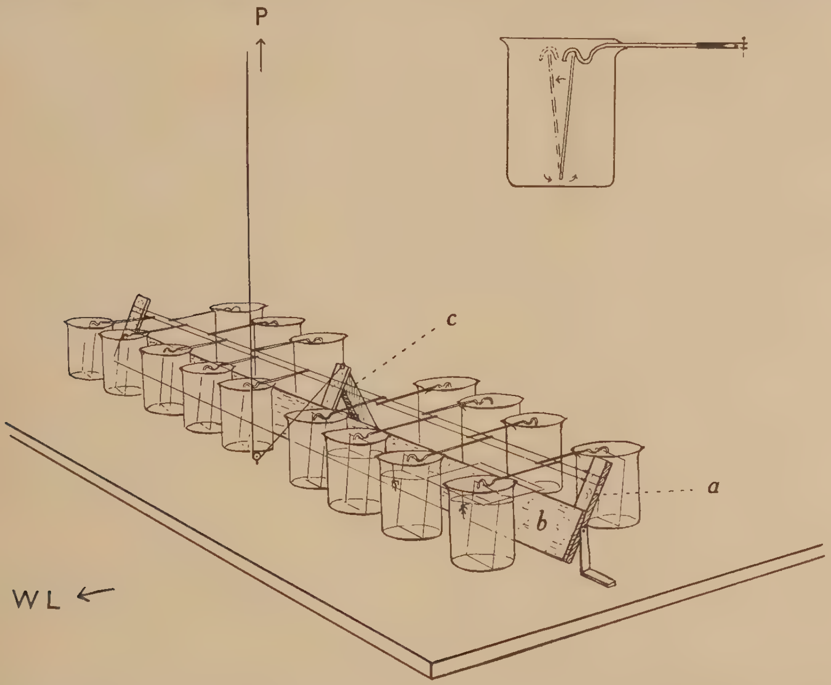


Fig. 12. Diagram showing arrangement of beakers with rocking plates for keeping hydroids. For full description see text. *a*, wooden upright; *b*, horizontal wooden batten; *c*, stopper; *P*, to plunger jar wire; *WL*, direction of window light. In the top right-hand corner is shown an enlarged drawing of a beaker and method of attachment of rubber tube to wire. (Del. F.S.R.)

The whole battery is set up on a bench about 14 ft. from a north window (Fig. 12 *WL*). Excessive plant growth is thus avoided. The colonies of hydroids are hung on silk threads just below the water surface on the side of the beaker nearest the window. An abundant supply of fine animal plankton is put at regular intervals into each beaker. Most of these animals being positively phototropic immediately collect near the surface on the lightest side of the beakers and are soon caught by the hydroid polyps. With a continuous supply of food the colonies grow very quickly and can be kept alive as long as required. Some of our colonies have remained thus over a year, the polyps dying down and regenerating at intervals.

There appears to be no necessity of changing the water, though at times it may be advantageous to do so to revive colonies that appear unhealthy, or if the accumulation of dead food organisms on the bottom becomes too great. As, however, the water can be easily changed, we have made a practice of doing so at regular intervals to ensure the best conditions possible. Up to the present most of the hydroids grown in these beakers have been somewhat sessile unbranching forms, and their growth has been quite normal and sessile. Whether the branching species will grow in their typical forms remains to be seen. This will probably depend upon an abundant food supply and on the hydroid itself hanging free from the side of the beaker. A single polyp of *Bougainvillia muscus* soon sent stolons on to the beaker side, and a creeping colony as described by Browne (1907) was quickly formed. In the centre of the colony, however, many of the polyps started to branch and grow upwards; these developed into quite typical growths of the *B. fruticosa* type.

In rearing primary polyps from medusae the substratum for the settling of the planulae may be of importance (see Day and Wilson, 1934). We have reared first polyps from the following species of medusae: *Steenstrupia rubra*, *Bougainvillia britannica*, *Turritopsis nutricula*, *Rathkea octopunctata*, *Amphinema dinema*, *Laodicea undulata*, *Mitrocomella brownei*, *Phialidium hemisphericum*, *Phialella cymbaloides*, and *Octorchis gegenbauri*. The planulae of all of these apparently settled without difficulty on glass except *Bougainvillia britannica* and *Rathkea octopunctata*, and possibly *Octorchis*. Of these the planulae of the first settled on a piece of smooth shell, but the polyps did not develop far enough to become distinctive. The settling of *Rathkea* planulae in detrital masses and rough hollows in the stem of *Eunicella* have already been mentioned. Planulae have also been obtained from *Lizzia blondina*; these would not settle on glass, and at the time no other substratum was offered; no doubt better success would have been obtained with a suitable substratum.

In order that the medusae may give successful results they should be brought into the laboratory in as good a condition as possible. It is best to pick the medusae out from the rest of the plankton catch on board as soon as the net comes up. Even then it was at first found that a high percentage were dead or dying at the end of the day when brought into the laboratory. On these occasions the medusae had been kept in breffits* filled with water. If the breffit was kept standing in the cool, with its lid on, the medusae sank to the bottom after a short time and soon became unhealthy. If placed under circulation with stramin tied over the opening and the sea-water jets playing on it, the medusae became damaged by air bubbles sticking to the umbrella surface.

It was found, however, that if the breffit were filled only to one-quarter of its capacity and then, with lid on, placed floating on its side in the circulation baths, the medusae remain in excellent condition. In this way the medusae were prevented from lying on the bottom because the breffit was continually rolling over with the motion of the ship or by the sea-water jets playing on it. Medusae picked out on board and kept in this manner were alive and active when brought into the laboratory and in such good condition as to remain alive many days in finger bowls of outside sea water until their gonads ripened.

SUMMARY

The development of the hydroid of *Amphinema dinema* (Péron & Lesueur) has been followed in the laboratory until the production of young medusae and the hydroid identified as *Perigonimus serpens* Allman.

The hydroid of *Amphinema rugosum* (Mayer) is described for the first time. It is very similar to *P. serpens* but more robust.

The hydroid has been reared from *Rathkea octopunctata* (Sars); it is very minute and the hydranths possess a single whorl of long filiform tentacles.

A small *Cuspidella* hydroid was reared from *Mitrocomella brownei* (Kramp).

Certain points in the synonymy of these species are discussed.

An account of the methods of rearing used is also given.

REFERENCES

ALLMAN, G. J., 1863. Notes on the Hydroida. *Ann. Mag. Nat. Hist.*, Ser. 3, Vol. XI, pp. 1–12.

—— 1872. *A Monograph of the Gymnoblastic Hydroids.* Ray Society.

BROOKS, W. K., 1883. Notes on the medusae of Beaufort, N.C. Part II. *Johns Hopkins Univ. Stud. Biol. Lab.*, Vol. II, XXXIV, pp. 465–75.

BROWNE, EDWARD T., 1898. On keeping medusae alive in an aquarium. *Journ. Mar. Biol. Assoc.*, Vol. V, pp. 176–80.

—— 1907. A new method for growing hydroids in small aquaria by means of a continuous current tube. *Journ. Mar. Biol. Assoc.*, Vol. VIII, pp. 37–43.

—— 1910. Coelenterata. V. Medusae. *National Antarct. Exped.* 1901–1904. *Nat. Hist.*, Vol. V, *Zool. and Bot.*, pp. 1–62.

CANNON, H. GRAHAM, 1937. A new biological stain for general purposes. *Nature*, Vol. 139, No. 3517, p. 549.

DAY, J. H. & WILSON, DOUGLAS P., 1934. On the relation of the substratum to the metamorphosis of *Scolecolepis fuliginosa* (Claparède). *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 655–62.

GOSSE, PHILIP HENRY, 1853. *A Naturalist's Rambles on the Devonshire Coast.* London: John van Voorst.

---

* Glass jars holding *ca.* 2 l. of water.

HAECKEL, ERNST, 1879. *Das System der Medusen.*

HARTLAUB, CLEMENS, 1897. Die Hydromedusen Helgolands. *Wiss. Meeresuntersuch.*, N.F. Bd. II, Abt. Helgoland, Heft 1, x, pp. 449–512.

—— 1914. *Nordisches Plankton.* Lief. 6, XII, Craspedote Medusen. Teil 1, Leif. 3, Familie IV, Tiaridae, pp. 237–363.

HINCKS, THOMAS, 1868. *A History of the British Hydroid Zoophytes.* London: John van Voorst.

—— 1877. Contributions to the History of the Hydroida. *Ann. Mag. Nat. Hist.*, Ser. 4, Vol. 19, pp. 148–52.

KRAMP, P. L., 1932. A revision of the medusae belonging to the family Mitrocomidae. *Vidensk. Medd. Naturh. Foren. Køjb.*, Vol. 92, pp. 305–83.

MARINE BIOLOGICAL ASSOCIATION, 1931. Plymouth Marine Fauna, 2nd Edition.

MAYER, ALFRED GOLDSBOROUGH, 1900. Descriptions of new and little-known medusae from the western Atlantic. *Bull. Mus. Comp. Zoöl. Harvard*, Vol. XXXVIII, No. 1, pp. 1–9.

—— 1910. *Medusae of the World.* Vol. 1. *Hydromedusae.*

MOTZ-KOSSOWSKA, S., 1905. Contribution à la connaissance des Hydraires de la Méditerranée occidentale. I. Hydraires gymnoblastiques. *Arch. Zool. Exp. Gén.*, Sér. 4, Tome 3, pp. 39–98.

PÉRON & LESUEUR, 1809. Histoire générale et particulière de tous les animaux qui composent la famille des Méduses. *Ann. Mus. Hist. Nat. Paris*, Tome XIV, pp. 312–66.

RICHIARDI, S., 1880. Contribuzioni all fauna d'Italia. III. Idroidi del Mare della Toscana. *Catal. Gener. Sezione Ital. Espos. Intern. Pesca Berlin*, pp. 154–5.

RITTENHOUSE, SAMUEL, 1910. The embryology of *Stomotoca apicata*. *Journ. Exper. Zool.*, Vol. 9, No. 2, pp. 333–48.

RUSSELL, F. S., 1936. On the hydroid of *Laodicea undulata* (Forbes & Goodsir). *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 581–8.

SARS, M., 1846. *Fauna Littoralis Norvegiae*, 1, pp. 1–94. Christiania.

STECHOW, E., 1923. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. *Zool. Jahrb. Jena* (*Syst.*), Bd. 47, pp. 29–270.

VAN BENEDEN, P.-J., 1866. Recherches sur la Faune Littorale de Belgique. *Mém. Acad. R. Belg.*, Vol. XXXVI, pp. 3–207.

WINTHER, G., 1880. Fortegnelse over de i Danmark og dets nordlige Bilande fundne Hydroide. *Naturhist. Tidsskr.*, Ræk. 3, Bd. XII, pp. 223–78.

ON THE SIZE-CHANGES OF DIATOMS AND THEIR OCEANOGRAPHIC SIGNIFICANCE

By Walter Garstang, M.A., D.Sc.

Emeritus Professor of Zoology (Leeds); Lincoln College, Oxford

(Text-figs. 1–9)

The peculiar life history of diatoms—their gradual reduction in width during a series of binary fissions, and the periodic restoration of their original size after production of "auxospores"—lends itself well to biometrical treatment, and R. S. Wimpenny of Lowestoft has recently given a striking demonstration of the differences in size composition which the populations of a given species may exhibit, both seasonally and locally. His first study deals with *Rhizosolenia styliformis*, and by a single example he has shown that small samples of the local populations may give decisive help in tracing the origin and movements of the dense patches of this diatom which accumulate near the Dogger Bank in certain years (1936, pp. 29–60; also Savage & Wimpenny, 1936, p. 23).

This aspect of the subject, however, was not the main object of Wimpenny's study, and he did not pursue it to the full extent of his material. He noted the existence of separate "large (i.e. wide) and small (i.e. narrow) populations", as well as the prevalence of bimodal populations at one time and of unimodal populations at another, but his main concern was an attempt to relate changes in average width to physical conditions. He claims that, in spite of the normal tendency of the diatoms to decrease in width as a consequence of repeated fission, the average width of the population tends to increase ("in each year", p. 38) during periods of rising temperature, or during periods of drift from regions of lower to regions of higher temperature. To account for this supposed relation he has recourse to a theory of selection, increase of temperature being held to favour survival of the wider diatoms.

This complex proposition is put forward quite tentatively, but is believed to be in harmony with the distribution of wide and narrow diatoms in warm and cold areas generally, a separate question which I have not examined. But the special propositions advanced with regard to *Rhizosolenia* are soon seen to have no adequate basis. The alleged correlation between average size and temperature breaks down at several points when the probable errors are taken into account, and the valid coincidences admit of much simpler explanations. In a region of intrusive and eddying waters, Wimpenny disregards the inevitable mixture of local populations, and most unaccountably, although he admits the upper size group in his bimodal samples to be the recent product of an auxospore generation, the rise of this generation is overlooked, and the resultant increases of size are included among his evidences of "selective survival". So far from there being a seasonal tendency towards increase of size, his samples show that in the main area of his investigations the size went up steadily during the summer of 1933 after an auxospore rejuvenation (though auxospores were not directly observed), and steadily down throughout 1934, during the succeeding phase of repeated fission. The failure to observe auxospores in either of the three years (p. 40) may be attributable to the fact that during the most favourable period, from mid-July to mid-September, no samples were taken.

It is, in fact, the regularity of the life cycle, its long duration (at least two, possibly three years), and its contrasted phases, which render the biometry of diatoms so admirably suited to oceanographic ends, and I believe Wimpenny's introduction of it in planktonic study may lead to fruitful developments. With due precautions the measurement of diatoms may yield precise indications of water conditions, water movements, and water mixture. In this belief I venture to submit a brief alternative treatment of Wimpenny's data, not so much to establish any particular propositions, as to indicate what kinds of problem may be brought to solution by the examination of samples suitably distributed.

Wimpenny's samples, twenty-two in number, were nearly all obtained by vertical hauls in the more or less dense "patches" already described for 1932 by Savage & Hardy (1935, pp. 31–4) and for 1933–4 by Savage & Wimpenny (1936). They are mostly limited to 100 specimens from each station except in 1933, when half the samples were increased to 300. The curves show that when the population is homogeneous the lower number is fairly representative, but when it consists of two generations, or of a mixture of two populations with different modes, the jagged nature of the curves shows this number to be inadequate for comparative purposes. In future work the standard sample should consist of not less than 200 individuals.

At one station (K 12), off the Outer Dowsing in October 1933, there is a check on the reliability of a sample in the fact that a horizontal haul at mid-water (10 m.) was sampled as well as a vertical haul, and 100 measurements are recorded for each. Both curves have the same mode (at 20 units) with practically the same frequency (24, 25%), but the vertical sample has a "shoulder" on the lower side of the mode (at 17), and the horizontal one a larger shoulder on the upper side (at 22–23), so that the average width is appreciably less for the former than for the latter (18·96 as against 20·16—calculated from Table II, p. 56). Wimpenny gives the average width for the station as 19·00 (p. 38), but as he denies the existence of any "marked differences of size" at different depths in the Southern Bight (p. 37), the variation revealed in two samples of a fairly homogeneous population shows the necessity of allowing an appreciable margin of error for the average size of the samples generally. The question, however, of a possible stratification in the vertical distribution of the different sizes ought not to be left without evidence.

In the summary account which follows I have retained Wimpenny's size units, which are stated to be approximately equal to 4μ. The curves for all the samples have first been drawn separately, but when two or more curves for the same time and area show the same essential features, I have here substituted a single representative curve based on a combination of the samples, so as to eliminate the greater irregularities due to small numbers. In two cases only (1933, F 5, VII; J 5, IX), where combination was impossible, erratic single curves have been smoothed. All the curves of size are percentage curves. The three years are dealt with separately, and in each year the curves for the same region are superimposed, so as to bring out more easily the seasonal changes shown by the samples.

1932

Three samples were measured in October from a dense patch south of the Dogger, the positions and movements of which are fully described by Savage & Hardy (1935, figs. 19–21). Its western edge was located on October 14 30 miles south of the South-west Spit of the Dogger, and in a fortnight had moved 50 miles east, with its axis extended north-east for an additional 70 miles at least. The samples came from three stations, 60 miles apart, along this track, say *A*, *B*, and *C* from west to east, the sample from *A* (Wimpenny's H.Q.) being a fortnight earlier than those from *B* (J 26) and *C* (J 20). The erratic curves of size are given separately by Wimpenny, but *A* and *B* differ from *C* in being essentially bimodal, with their main features in common, so in my treatment these two have been combined (Fig. 1).

The average widths of the three samples are given by Wimpenny as 15·3, 16·0, and 16·8; the temperatures as 12·23°, 12·24°, and 12·44° respectively. This "progression of the means", in connexion with the "advance" of temperature, is specially cited by Wimpenny as one of his chief examples of selective survival ("this apparent selection of the wider cells as the patch drifted into areas of higher temperature", p. 40). The curves, however, contain clear evidence, not of selection, but of a progressive mixture of two divergent populations, a bimodal population (*X*), strongest in the west, with a major mode at 12–13, a minor mode at 19–22, and a trough at 17–18, and a unimodal population (*Y*), strongest in the east, with a mode about 17. This size is scarcely represented in *A*, but forms a shoulder on the upper side of the major mode in *B*, and the principal peak in *C*. Minor differences between the curves for *A* and *B* suggest that neither of the primary populations was quite constant from west to east, particularly the unimodal one, which at *A* probably had its peak at 15 or 16 as indicated by the lower position of the shoulder (at 16 instead of 17) and by the wider "trough" (at 17–18 instead of 18).

A rough attempt to reconstruct the observed populations by mixture of two hypothetical primaries is represented in Figs. 2 and 3. *X* and *Y* are two possible "primaries", *X* being bimodal and for simplicity assumed to have been uniform throughout, *Y* being unimodal and assumed to be represented in the west (A) by a similar population with its mode one unit lower (Y'). A 2 : 1 mixture of the two primaries, with X predominant at A and B,

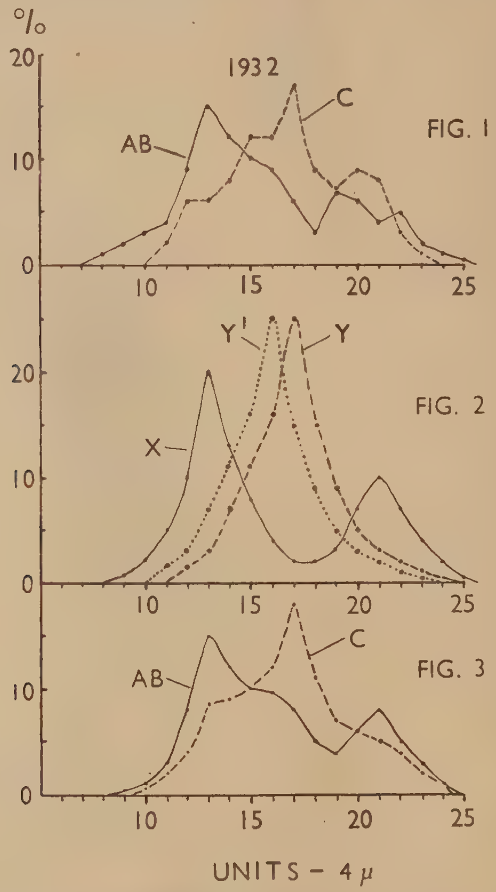


Fig. 1. Frequency curves of variation in width of *Rhizosolenia styliformis* at stations $A+B$ (combined) and C in October (percentages). AB = Wimpenny's H.Q. + J 26. C = Wimpenny's J 20.
Fig. 2. Hypothetical pure populations supposed to be mixed in Fig. 1.
Fig. 3. Empirical mixtures of X with Y' (west) and Y (east). $AB=(2X+Y')+(2X+Y)$. $C=X+2Y$.

and Y predominant at C, may then be expressed by the following combinations:

$$A=2X+Y',$$
$$B=2X+Y \text{ or, more closely, } 2X+\frac{Y'+Y}{2},$$
$$C=X+2Y,$$

or, combining the formulae for A and B, in conformity with Fig. 1,

$$A+B=4X+Y'+Y,$$

$$C=X+2Y.$$

The results of the last two combinations, after reduction to percentages, are seen in Fig. 3, and should be compared with Fig. 1. It will be admitted, I think, that this empirical synthesis comes sufficiently near the mark to justify my interpretation of the populations sampled as mixtures of two purer populations of the X and Y type in something like the proportions given.

There are unfortunately no available data outside the patch to show the source or distribution of the two populations of which it appears to be compounded, although specimens collected by Prof. Hardy's continuous recorders during September and October would probably fill the gap if measured (cf. Savage & Hardy, 1935, fig. 21). The different constitution of its eastern "head" and western "tail" seems to indicate that it was formed either (1) by the fusion of two separate patches, ultimately east and west, or (2) along a line of convergence of northern and southern waters, which brought successive northern and southern populations into contact and mixture. The coexistence of two divergent populations, but without serious mixture, was a striking feature of the samples in October 1933. In the following autumn (1934) we shall see that mixed populations were again conspicuous on the central grounds, but this time in the same phase with nearly related modes at 15 and 17.

1933

In 1933 there are samples for July, September and October off the western edge of the Dogger, two October samples from the Bank itself, and eight October and November samples from a wide area south of it. The last series is so uniform that the samples have been united to form two large arrays representative of the two months. The curves (Figs. 4–6) for the three areas follow the order here given, those for each area being superimposed.

In the first area two of the samples (F 5, VII; J 5, IX) are small (100), yielding very jagged curves, which would be confusing if superimposed. I have therefore smoothed them by readjustment of the frequencies as follows:

Widths (=4 μ)	...	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
F 5, VII	Observed	1	4	7	6	9	20	18	5	6	5	2	1	3	4	5	3	–	1	–	=100
	Smoothed	1	3	6	9	14	18	16	8	5	3	1½	1	3	4	4	2	1	½	–	=100
J 5, IX	Observed	–	–	2	8	9	10	5	4	3	1	5	4	14	8	13	5	9	–	–	=100
	Smoothed	–	–	2	5½	9	10	7	4	2	1	3	7	11	12	11	8	5	2	½	=100

The third sample (L 30, X) was larger (300). Its curve (and that of every other sample, or combination of samples, in this account) is unsmoothed.

All the curves for this year show a pronounced bimodality, as Wimpenny (p. 32) observed. The two groups are here assumed to mark successive auxospore generations, the old generation having a mode at 11–12, the new one at

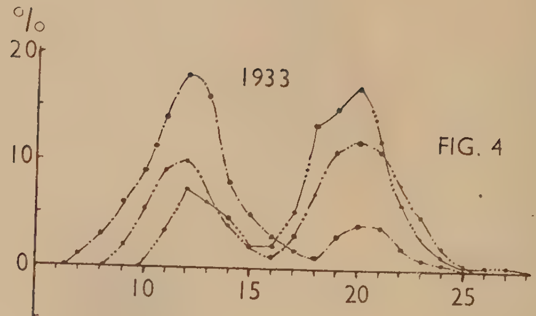


FIG. 4

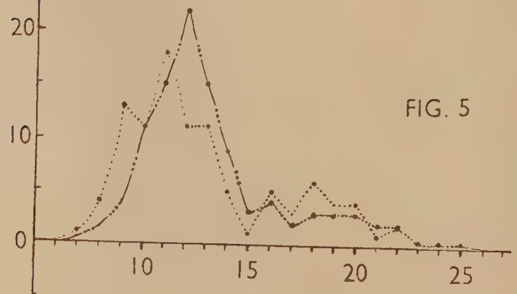


FIG. 5

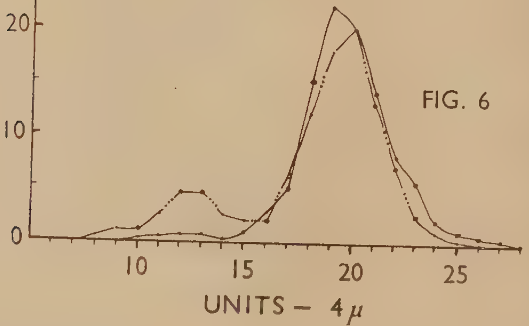


FIG. 6

Fig. 4. West of Dogger. July (F 5), —·—·—, Sept. (J 5), —··—··—, both smoothed. October (L 30), unsmoothed, —···—···—.

Fig. 5. Dogger Bank, October. Combined samples (K 28+L 35),—···—···—. K 28 alone, ········ .

Fig. 6. Coastal belt, South of Dogger. October, five samples combined, —···—···—. November, three samples combined, —— .

19–21. There is a difference of phase, but not of type, between the curves of the first and third areas, and, as the first includes the earliest samples (VII, IX, X), and the third the latest (X, XI), the two together illustrate all the stages in the waning of an old generation and the rising of a new one. In July (F 5) the old generation far exceeded the new one in frequency, in September (J 5) the new generation had slightly out-topped the old one, and by October the old and new generations had everywhere changed places as regards frequency.

The two curves for the third (or southern) area (Fig. 6) have been yielded by combinations of the following samples; duly weighted:

October: K 1 (100), K 12 (200), K 13 (100), L 9 (300), L 15 (300).

November: "Onaway", 8 (100), 9 (300), and "Tea Kettle Hole" (100).

Fig. 6 shows how completely the old generation had been replaced in November by the new one, and that the mode of the latter had already receded from 20 to 19, doubtless as a consequence of repeated fissions.

The second or Dogger group (Fig. 5) consists of two samples only, both from dense October patches on opposite sides of the Bank, viz. K 28 (100) and L 35 (300). The former yields a jagged curve, and has been combined with the other to form a single representative curve, but it has also been added to the figure as an indication of the slight differences involved, its mode being a unit lower than that of the other. Geographically the three samples from the first area especially L 30, are barely distinguishable from the Dogger samples, being only 20 or 30 miles south or south-west of K 28; but, as shown by the curves, the October populations of the two areas were very different, the new generation on the Dogger being no further developed than it was in July in the western group, and its principal, or old, generation having the same mode (12), in spite of intense proliferation. The question of divergent populations in close proximity is thus raised again in a new form: Are we to regard the October phase on the Dogger as merely the July population retarded in development, or as an alien population from some other region?

K 28 was taken near the south-west edge of the Dogger shoal a fortnight before L 35, the position of the latter station being 50 miles farther east, off the south-east edge of the Bank. Savage & Wimpenny give hydrographic reasons for regarding the two stations as representing successive centres of the same patch, which they believe had rounded the southern extremity of the Bank in the meantime. If the mode of K 28, however, can be relied upon, as seems probable, this view is in opposition to the biometric evidence, since K 28 was in a later, not an earlier, phase of size reduction. The conditions, in fact, partially reproduce those of the patch of 1932, but without the complexity of a mixture of populations, K 28 recalling *A*, and L 35 recalling *B* or *C*, in which the mode of the *Y* population was higher than it was at *A*, and therefore not directly derivable from it. In this case also the eastern and later patch (L 35, October 22) cannot be regarded simply as the western patch (K 28, October 13) which had shifted its position. If K 28 was its nucleus, it must have picked up a great preponderance of other diatoms with the higher mode in transit. More probably an eastern patch was already in existence at the time of the K cruise, but just beyond its range (cf. Savage & Wimpenny, figs. 2 and 4), and was joined by the western patch during the intervening fortnight. Hardy's recorder sampled two strong patches on the Hull-Skagerak line, along the south-east edge of the Dogger, on October 14, thus supporting this suggestion. One may remark again how useful it would be to have their measurements (Hardy, 1935, fig. 4).

As regards their origin, the patches may have been formed within successive swirls off the Dogger Bight, but, in view of their great density (over 500,000 per m.^{3}) it is impossible to identify them with the similar population found on the South-west Spit (F 5) in July. To allow for their subsequent proliferation, their modes in July must have been at least two units higher (cf. the seasonal changes in the mode during 1934 below), so that the hypothesis of a different origin is probable. They may, in fact, have been descendants of the same stock which contributed the *Y* element to the patch of 1932, though there is nothing but the calculated correspondence of their modes to support the suggestion. In both cases this stock and its descendants were presumably of northern origin.

Similarly, the *X* element of 1932, with its new generation still rudimentary in October, may have been part of a western population which survived to initiate the great bimodal population west and south of the Dogger in 1933.

1934

For 1934 the samples (all 100) also fall into three groups, but not quite the same as for 1933: (1) the North-west Deeps (Firth of Forth Swirl), (2) the Dogger region, and (3) the coastal belt, the last with only two stations, G 5 off Flamborough Head in July, and M 21, 50 miles north-west of Texel in October.

The first group (Fig. 7) is especially interesting, since it throws light on conditions in a region farther north than was sampled in 1932 and 1933. Two samples (C 19, V and E 5, VI), with modes at 10 and 11 respectively, have been combined to represent the spring condition. A third (M 3) was taken in October. The increase in average width (10·94 in May, 12·50 in October) is included by Wimpenny among his examples of increase of size with temperature. The spring population, however, was unimodal, and consisted of old generation diatoms only; the autumn population was bimodal, with two cusps of almost equal frequencies at 7 and 16. These modes are lower than those of the bimodal populations farther south in 1933, but the interval is the same. They clearly mark a new generation in the making.

Comparison with Figs. 8 and 9 shows how completely this area differed from the whole of the southern region in its population phase at any time, thus showing, as Wimpenny pointed out, that the *Rhizosolenia* patch that was forming off the western edge of the Dogger in June (E 17) could not possibly

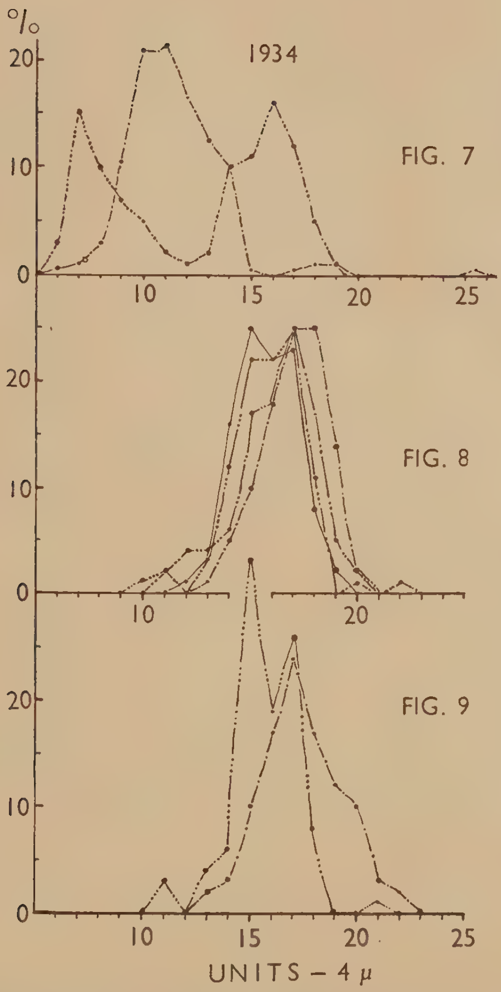


FIG. 7

FIG. 8

FIG. 9

Fig. 7. North-west Deeps (Firth of Forth Swirl). May (C 19) and June (E 5) combined, —·—·—. October (M 3), —···—.

Fig. 8. Dogger Bank. June (E 17), —·—·. Sept. (L 17), —··—. Oct. (M 14), —···—. Nov. (On. 6.) ——.

Fig. 9. Coastal belt. July (G 5), off Flamborough, —·—·—. October (M 21), North-west of Texel, —···—···—.

be an offshoot from the northern population (E 5) (Savage & Wimpenny, 1936, p. 23).

Nevertheless, the two regions are probably not completely independent. The mode of the northern population in the spring (10–11) closely recalls that of the Dogger patch of the previous October (11–12), and the difference is no greater than can reasonably be attributed to the effect of successive fissions in the interval. As this Dogger population completely disappeared from the Bank during the winter (cf. Fig. 8), it was probably carried away to the north, and may well have been brought round to the Forth region in the wide anticlockwise circulation north of the Bank. Such a circuit might account for the irregularity shown by the two spring modes, that of the earlier sample (C 19) being actually a unit lower than that of the later one (E 5). Both curves also show a hump at 14, which betrays appreciable mixture with some unknown alien population.

The second and third groups show so much in common that they may be considered together. The second (Fig. 8) includes the following samples:

June	E 17	Mode 17–18.
Sept.	L 17	Mode 17, with "shoulder" at 15.
Oct.	M 14	Mode 17, with stronger shoulder at 15.
Nov.	On. 6	Mode 15, with shoulder at 17.

All four stations were on, or near, the southern shoal of the Dogger.

The third group includes:

July	G 5	Mode 17, with low shoulder at 19–20.
Oct.	M 21	Mode 15, with minor peak at 17.

The July station was off Flamborough Head, 30 miles from the South-west Dogger; the other was 50 miles south-east of the southern edge of the Dogger, half-way to Texel.

The September and all later samples show signs of extensive mixture between two nearly related populations with modes at 15 and 17 respectively. A study of the curves and of Savage & Wimpenny's charts leaves little doubt as to their history, although an additional sample or two from the southern belt would have been welcome. The mode at 17 was especially characteristic of the Dogger samples, that at 15 of the single southern station. In the former the shoulder at 15, rising steadily through September and October, ultimately in November surpassed the original mode in frequency. From its omission of the intermediate mode at 16 this change cannot have been the result of local proliferation, but marks an intrusive element. In September Savage & Wimpenny (1936, fig. 14) defined a great reniform patch pivoted on the south-west part of the Dogger and expanded southwards over a large area of the Norfolk banks, with two centres of density, a small one on the Dogger with a density maximum of 100,000 per m.^{3}, and a large one over the Norfolk banks with a maximum density of 300,000 per m.^{3} The patch arose by the fusion in July of two separate light patches which had apparently formed successively in the

Dogger Bight in June and been arrested in their movement eastwards (*loc. cit.*, figs. 10–12). The original population of both was probably identical, or nearly so (cf. E 17, G 5), but the greater rate of proliferation over the Norfolk banks already indicated would reduce the mode more rapidly in the southern patch, while in August–September the marked conditions of swirl (*loc. cit.*, figs. 13, 14) which followed their fusion would induce the observed mixture of the two populations. This would be more marked in the Dogger samples because of the greater density of the southern portion of the patch. In October the patch broke up again, or became highly ramified, and the larger southern portion drifted eastwards. M 21 sampled the western side of the drifted patch in October; L 17 sampled the northern centre of density of the united patch, M 14 and On. 6 the same part after the southern mass had separated.

The modes of the two spring samples (E 17 and G 5) at 17–18 seem clearly to affiliate both these populations to the autumn stock on the coastal belt in the previous year (M = 19–20). Savage & Wimpenny (1936, p. 25) have already attributed the wide distribution of this diatom in 1934 to the "scattering by water movements during the intervening months of the residue following the big flowering which took place in the autumn of 1933". It should be noted, however, as already remarked, that the dense patches on the edge of the Dogger in that year contributed practically nothing to the initial populations of 1934, either on the Dogger itself, or on the coastal banks. They must have been swept completely out of the region during the winter.

The sharp contrast between the Dogger and coastal modes in 1933, and the wide range of intermixture of less divergent populations in 1934 imply a considerable difference in the current systems of the two years, which Savage & Wimpenny have set out in great detail. The main difference between the two years, however, seems to be brought out more simply by the populations of *Rhizosolenia*. In 1933 the presence of a distinct northern population on the Dogger may be associated with the early invasion of saline northern water over the Bank, its prolonged duration there, and the pressure it set up against intrusion from the coastal waters, while in 1934 there was no such influx after July, consequently no northern population, and no resistance against encroachment. The Dogger and Norfolk banks were populated alike from the west, and early differences in the mode, caused by different rates of proliferation, were soon swamped by intermixture.

Summary of Population Changes, 1932–4

In the following table an attempt has been made to summarize the preceding survey by picking out the spring and autumn characters of the *Rhizosolenia* populations for each of the three main areas in each of the three years, and by bracketing together those populations which appear to have been connected by direct descent.

A thick inverted V indicates a normal unimodal population (Λ), the mode of which is given alongside in Wimpenny's units ($=4\mu$). A thick inverted W marks a bimodal population (ʍ), i.e. an old generation with low mode, and a new generation with high mode. A fraction preceding the letter *R* indicates roughly the amount of Regeneration which has taken place. Thus, ʍ $\frac{1}{4}R$ means a bimodal population in which the old generation still greatly preponderates; ʍ $\frac{1}{2}R$, one in which the old and new generations are approximately equal; ʍ $\frac{3}{4}R$, one in which the new generation preponderates, and the old generation is more or less obsolete. Mm = major mode.

	North-west Deeps (Firth of Forth Swirl)	Dogger Bank	South and west (coastal banks)
1932, X	?	Λ M = 16 – 17	ʍ $\frac{1}{4}R$, Mm = 13
1933, V–VI	?	?	ʍ $\frac{1}{4}R$, Mm = 12
1933, X–XI	?	ʍ $\frac{1}{4}R$, Mm = 11 – 12	ʍ $\frac{3}{4}$R, Mm = 20 – 19
1934, V–VI	Λ M = 11 – 10 ←	Λ M = 18 – 17 ←→	Λ M = 17 (VII)
1934, X–XI	ʍ $\frac{1}{2}R$, M = 7 + 16	Λ M = 17 (– 15)	Λ M = 15

It will be noticed that the population on the coastal banks seems to have been uninterruptedly continued from one season to another without any sign of marked invasions from without. Starting in October 1932 with a bimodal population in which rejuvenation had only recently begun, and the mode of the old generation stood at 13, the whole life cycle was still incomplete in November 1934, when the mode was 15. Assuming that it was completed in the spring of 1935 it required $2\frac{1}{2}$ years for its accomplishment. If we regard the coastal population accordingly as indigenous and self-maintained, although perpetually being carried away by the north-easterly drift, its annual renovation must depend on the persistence in the west of adequate residues of the previous year's stock.

On the Dogger Bank the population seems to have been continuous from October 1932 to November 1933, and during this period to have been quite independent of the stock on the coastal banks. A complete break then followed, and the new population in the spring of 1934 was indistinguishable at first from that on the coastal banks. A slight difference seems to have developed later, owing to local differences in the rate of proliferation, but from September onwards, as we have seen, there was incessant intermixture.

The fragmentary data for the North-west region are limited to the last year, which is unfortunate. In the spring of 1934 the initial stock, though slightly mixed with some other population, was closely similar to the Dogger population of the previous autumn. The chief difference between the two strains is that the Dogger population was already showing the beginnings of a new generation in 1933 (Fig. 5), while that of the North-west Deeps, *though showing vestiges of such a start*, did not enter upon this phase with any vigour until after June 1934. If, as suggested, the North-west population was largely descended from the previous Dogger stock, the intervening winter, and a prolonged northern circuit, must have completely checked regeneration by auxospores, and a further period of proliferation must be assumed to have set in to account for the reduction of the mode from 11–12 to 10–11. We know that this proliferation actually took place (Savage & Wimpenny, 1936, p. 11, fig. 9). It is also very noticeable that, after rejuvenation was resumed, both modes of the resultant population were markedly lower than at the corresponding phase on the coastal banks during 1933. This reduction may have been a further consequence of the enforced stoppage of rejuvenation during the winter and the additional proliferation which ensued before the season of auxospore formation had arrived. It may, on the other hand, though improbably, mark a permanent racial difference, which only additional observations can settle.

Further investigations in this area are clearly desirable in order to correlate with conditions on the Dogger. It seems highly probable that in "Atlantic" years, when northern waters extend southwards over the bank, a close relation will be recognizable between the population phases of the Dogger and of the North-west Deeps.

But it would perhaps be as well before detailed observations are made that the biology of *R. styliformis* should be more closely studied. It is, for instance, not known to what extent or at what times resting spores are formed, or whether diatoms arising from resting spores begin at the same size as those from which the spores were formed. If they were of different size the wrong conclusion that they had been transported from elsewhere might result. In any case I hope to have shown that with sufficient knowledge of the biology of *Rhizosolenia* the start made by Wimpenny on measurements of diatoms may lead to the foundation of useful indicators of water movements. In the open ocean also, where mixture may be less troublesome than in the North Sea, the proof of a long and well-marked life cycle in *Rhizosolenia* may ultimately yield a valuable timetable in problems of water transport.

SUMMARY

Wimpenny's measurements of *Rhizosolenia styliformis* (this *Journal*, Vol. XXI, pp. 29–60, 1936) are used to discuss the value of population curves of this species as indicators of water movements and mixture in the North Sea. His alleged correlation between average size and temperature is shown in this case to be untenable. On the coastal banks during 1933 there was a steady increase of size accompanying normal regeneration (bimodal curves), but this was complete by November, and in 1934, with fuller seasonal sampling, the size steadily diminished (all curves unimodal). The population phases on the Dogger and coastal banks were markedly divergent in 1933, but almost identical and intermixed in 1934, indicating a northern ("Atlantic") influx in 1933 and its absence in 1934. Off the southern edge of the Dogger in the autumn of 1932 a bimodal and unimodal population were variously mixed, the former showing relations to the coastal population of the following spring, the latter probably marking the intrusive northern element which persisted into 1933. The spring population of 1934 in the Firth of Forth Swirl (as already

noted by Wimpenny) was quite different from that farther south, both Dogger and coastal, the northern influx having then disappeared, but it showed significant relations to the Dogger population of the previous autumn.

REFERENCES

HARDY, A. C., 1935. The continuous plankton recorder. *Rapp. Proc. Verb. Cons. Int. Expl. Mer.*, Vol. XLV, p. 39.

SAVAGE, R. E. & HARDY, A. C., 1935. Phytoplankton and the herring. Part I, 1921–32. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. XIV, No. 2.

SAVAGE, R. E. & WIMPENNY, R. S., 1936. Phytoplankton and the herring. Part II, 1933 and 1934. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. XV, No. 1.

WIMPENNY, R. S., 1936. The size of diatoms. I. The diameter variation of *Rhizosolenia styliformis* Brightw. and *R. alata* Brightw. in particular and of pelagic marine diatoms in general. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 29–60.

NOTE ON SELECTIVE FEEDING BY *CALANUS*

By H. W. Harvey, Sc.D., M.A.
Hydrographer at the Plymouth Laboratory

The rates at which *Calanus finmarchicus* eat both carmine particles and the diatom *Nitzschia closterium* have been investigated by Fuller & Clarke (1936) and Fuller (1937). They found that the number of *Nitzschia* or of carmine particles, eaten by a *Calanus* in unit time, was proportional to the concentration of *Nitzschia* or of particles in the water. Lucas (1936) also found that *Neomysis* and *Eurytemora* ate *Nitzschia* at rates which were roughly proportional to the concentration of diatoms in the water over fairly wide limits.

During 1935 I had made, as part of another investigation, three experiments on the rate at which *Calanus* eat diatoms of larger size. This happened much more rapidly than Fuller found to be the case with suspensions of *Nitzschia*. Meanwhile Lowndes (1935) had concluded, from direct observations, from the anatomy of their mouth-parts and from observations by Lebour and Marshall, that *Calanus* should be able to catch and select food. He concluded that *Calanus* does not depend entirely upon its (automatic) filtering mechanism for all the food it obtained.

The quantitative data which I had collected in these three experiments, in conjunction with those published by Fuller & Clarke (1936, 1937), were suitable for examining this contention. They suggested that the animal when fed with diatoms of moderate size selected by catching the species it preferred, while it automatically filtered the minute *Nitzschia*. With these possibilities in view, experiment N 90 was made in order to link up the three experiments with the numerous experiments made by Fuller (1937).

EXPERIMENTAL

Stages V and VI of *Calanus finmarchicus* were recognized by their larger size, transferred from a tow-net catch into filtered sea water, to which some particular species of diatom was added as food, and were kept for some days. At the start of the experiment the required number were transferred to a litre beaker half-filled with sea water to which diatoms had been added from a culture. These diatom suspensions were made the previous day and kept overnight in the dark, in order that the number of diatoms increasing by division during the course of the experiment should be reduced to a minimum.

After adding the *Calanus* the water in the beaker was kept stirred by means of an oscillating glass plate. This proved an efficient method of stopping any diatom or animal settling on the bottom. It has since been used for rearing hydroids, and details of the apparatus are shown by Rees & Russell (1937).

During the experiment the beakers were kept in the dark in order that the diatoms should not divide.

Samples of the water in the beakers were taken for counting the diatoms, which was done by the sedimentation method using an inverted microscope.

Experiment A. *Calanus* were transferred from a tow-net catch on April 17 to filtered sea water to which *Ditylium brightwellii* was added daily. After 8 days seven *Calanus* were transferred to a beaker containing 425 c.c. of a mixture of *Lauderia borealis* and *Ditylium*, in 5·9 c.c. of which 464 *Ditylium* and 1290 *Lauderia* were counted. After 7 hr. in the dark a sample was withdrawn and 8·2 c.c. found to contain 191 *Ditylium* and 1386 *Lauderia.*

Experiment B, carried out at the same time as A, differed in that the *Calanus* were fed on *Lauderia* for the 8 days previous to being transferred to 355 c.c. of the mixed culture. A sample of this was withdrawn after 7 hr. and 313 *Ditylium* and 1500 *Lauderia* were counted in 11·0 c.c.

Experiment C. *Calanus* caught on March 7 were fed on *Lauderia* for a week and then transferred to a mixture of *Lauderia* and *Chaetoceros* sp., containing sixteen *Lauderia* per c.c. After 48 hr. in the dark the population of *Lauderia* was reduced to 1·9 per c.c., and after 3 days to 0·37 per c.c. without any considerable reduction in the *Chaetoceros* population.

Experiment N 90. *Calanus*, stages V and VI, were transferred from a tow-net catch into filtered sea water and kept for 3 days. On June 6 they were again transferred and a small amount of both *Lauderia borealis* and *Nitzschia closterium* forma *minutissima* was added as food. On June 7 twenty-five individuals were transferred to a beaker containing 500 c.c. of a culture of *Lauderia* and *Nitzschia*. A second beaker was also half-filled with the culture, and both were kept in the dark with moving plates to keep them stirred. Samples of the water were taken out after 4, $10\frac{1}{4}$ and 24 hr., and the cells in measured volumes counted.

At start of experiment:	353 *Lauderia* were counted in 2 c.c. 158 *Nitzschia* were counted in 1 mm.^{3}
After 4 hr. in beaker with *Calanus*:	290 *Lauderia* were counted in 3 c.c. 157 *Nitzschia* were counted in 1 mm.^{3}
After $8\frac{1}{4}$ hr. in beaker with *Calanus*:	94 *Lauderia* in 3 c.c.
After 24 hr. in beaker with *Calanus*:	5 *Lauderia* in 3 c.c. 123 *Nitzschia* in 1 mm.^{3}
After 24 hr. in beaker without *Calanus*:	151 *Nitzschia* in 1 mm.^{3}

If the number of diatoms caught and eaten by a *Calanus* is directly proportional to the population density or concentration of the diatoms, then

$$P_2 = P_1\, e^{-kt},$$

where P_1 is the initial concentration of diatoms, P_2 the concentration after time t, and k is a constant. Further, if v is the volume of water per *Calanus*, then vk is the volume of water "swept free" from diatoms by one *Calanus* in unit time.

Collecting the data for the rate at which *Calanus* eat the various species we obtain the following values for vk:

	P_1 Initial concentration diatoms per c.c.	P_2 Concentration after t hr. diatoms per c.c.	t hr.	v Vol. per *Calanus* c.c.	vk Volume "swept free" by one *Calanus* in 1 hr. c.c.
		Lauderia borealis			
Experiment A	220 ± 6	168·5 ± 4·5	7	61	2·2
Experiment B	220 ± 6	136 ± 3·4	7	51	3·3
Experiment C:					
First 48 hr.	13	1·9	48	50	2·0
Subsequent 24 hr.	1·9	0·37	24	50	3·1
Experiment N 90:					
First 4 hr.	176·5 ± 9·4	97 ± 8·5	4	20	2·9
Subsequent 6¼ hr.	97 ± 8·5	31 ± 3	6·25	20	3·6
Subsequent 13¾ hr.	31 ± 3	1·6 ± 1·2	13·75	20	4·0
		Ditylium brightwellii			
Experiment A	79 ± 3·5	23·3 ± 2·5	7	61	10·0
Experiment B	79 ± 3·5	28·4 ± 1·7	7	51	7·0
		Nitzschia closterium forma *minutissima*			
Experiment N 90	154,500 ± 8,800	123,000 ± 11,000	24	20	0·19 (0·31–0·05)
Fuller (1937, p. 234)			Mean value		0·045
		Carmine particles			
Fuller & Clarke (1936, p. 318)			Mean value		0·23

The experimental error in counting the diatoms amounts to the square root of the total number counted. This was calculated and reduced to terms of diatoms per c.c. as shown in the table.

A reasonable agreement is even shown between the values obtained for *Nitzschia* by Fuller and in Experiment N 90, in which the experimental error was necessarily large. The range of values of vk (0·31–0·05) calculated from P_1 and P_2 after applying the experimental errors, and of those obtained by Fuller (0·07–0·025) overlap.

I am indebted to Mr G. M. Spooner for a statistical examination of some of the data. This showed that the difference between Experiments A and B is just significant. They can be stated more clearly in the following form:

EXPERIMENT A. *Ditylium*-fed *Calanus* ate in 7 hr.

23·4 ± 3·5 % of the *Lauderia*
70·5 ± 6·3 % of the *Ditylium*
in the mixed culture.

EXPERIMENT B. *Lauderia*-fed *Calanus* ate in 7 hr.

38·4 ± 3·4 % of the *Lauderia*
64 ± 5·9 % of the *Ditylium*
in the mixed culture.

It is not suggested that this pair of experiments, standing alone, shows that the species eaten previous to the experiment had affected the animals' preference when presented with a mixture.

It is, however, clear that a very significant difference existed between the rate at which the three diatoms were "eaten".

Since the feeding rate of *Calanus* is now being investigated elsewhere, no further experiments were made.

Fuller (1937) suggests that the *Calanus* are probably able to capture large objects more readily than small ones. It is noteworthy that the *Ditylium*, which were most readily captured, were twice or three times the size of the *Lauderia*, while *Nitzschia* is extremely small compared with either.

I have pleasure in acknowledging not only help from Mr Spooner in treating these data, but gifts of diatom cultures from Dr H. C. Gilson and Dr Fabius Gross, and help by Dr M. V. Lebour in separating the stages of *Calanus*.

REFERENCES

Fuller, J. F. & Clarke, G. L., 1936. Further experiments on the feeding of *Calanus finmarchicus*. *Biol. Bull.*, Vol. 70, p. 308.

Fuller, J. F., 1937. Feeding rate of *Calanus* in relation to environmental conditions. *Biol. Bull.*, Vol. 72, p. 233.

Lowndes, A. G., 1935. The swimming and feeding of certain Calanoid Copepods. *Proc. Zool. Soc. Lond.*, p. 687.

Lucas, C. E., 1936. On certain interrelations between phytoplankton and zooplankton under experimental conditions. *Journ. Cons. Int. Explor. Mer*, Vol. IX, p. 343.

Rees, W. J. & Russell, F. S., 1937. On rearing the hydroids of certain medusae with an account of the methods used. *Journ. Mar. Biol. Assoc.* Vol. XXII.

THE NEWLY HATCHED LARVA OF *SPIRONTOCARIS SPINUS* (SOWERBY) VAR. *LILLJEBORGI* DANIELSSEN

By Marie V. Lebour, D.Sc.
Naturalist at the Plymouth Laboratory

(Text-fig. 1)

On February 29 1937 the larvae of *Spirontocaris spinus* var. *lilljeborgi* were hatched out in the Dove Marine Laboratory by Dr H. O. Bull and sent to me for examination. As the larvae differ in certain important points from those of other species known and there is no published account of them, it seems worth while giving a short description, although the later larvae have not been identified and it was not possible to rear them further.

The parent was intermediate between the type *S. spinus* and the var. *lilljeborgi*, having the rostrum like the latter, but the dorsal spine on the third abdominal segment fairly prominent much as in typical *S. spinus*. The rostrum being regarded as the more important feature, the specimen is relegated to the variety.

Spirontocaris spinus is the type of the genus, but it differs considerably from those common British species which live closer inshore, leading up through *S. pusiola* to *S. occulta* and *S. cranchii* (see Lebour 1936). The larva of *S. pusiola* is not known (although Sars (1912) states that he has hatched it from the egg and that it closely resembles *Hippolyte*), but those of the inshore species *Spirontocaris occulta* and *S. cranchii* and several inshore species from California hatched by Needler (1933) all agree in certain features which may be regarded as typical for this group; they are in fact very closely related to *Hippolyte* which is essentially an inshore genus. *Spirontocaris spinus* var. *lilljeborgi* has a long rostrum in the newly hatched larva (absent in all the others and only appearing as a very short one in Stage II) and the endopod of the antenna, usually a single rod terminating in a setose spine, bears on its outer side a long plumose seta. It is also larger and further developed than any of the inshore species. Stephensen (1912, 1916, 1935) described several larvae of *Spirontocaris* from the deep water round Greenland, all of which hatch in an advanced stage, as is also the case in *S. polaris* taken from the egg by Krøyer (1842). Thus the more open water species are more advanced in hatching and tend to have their larval life abbreviated, whilst the inshore forms hatch in a less developed state and have a more or less prolonged larval life. Stephensen suggests that his larva No. 1 (1916) which he considers to be identical with his No. 1A

(1935) might belong to *S. groenlandica*, *S. gaimardi* or *S. spinus*; but it cannot be *S. spinus*, as it does not agree with those hatched from the egg. His larva No. 5 (1935) has a long rostrum but is obviously different from *S. spinus* and, as he suggests, very probably belongs to *Dichelopandalus leptoceros*.

Mr R. Elmhirst has hatched the larvae of *Spirontocaris spinus* var. *lilljeborgi* at Millport and Dr H. O. Bull has hatched them twice at Cullercoats. Their notes, which they kindly allow me to quote, agree in all essentials with mine. Elmhirst's specimens were hatched on March 29 1934. He states that the species breeds from December to April, and that the newly hatched larva are coloured bright red and yellow. The long rostrum and the seta on the antennal endopod are noted; also the rudiments of legs. Bull's first specimens were hatched on March 10 1934. He notes the same characters.

DESCRIPTION OF THE NEWLY HATCHED LARVA (Figs. 1 *a–d*)

The egg with the larva ready to hatch is 0·96 mm. by 1·2 mm. In the embryonic cuticle there are 6 + 6 spines on telson, the two inner setae enclosed in one envelope, as is usual in the Caridea. The newly hatched larva is 3·7 mm. long from tip of rostrum to end of telson. There is a tooth at the antero-ventral corner of carapace but no ventral denticulations. Lateral spines are present on abdominal segment 5. The anal spine is conspicuous as early as the first stage which is a characteristic of the genus. The telson is deeply excavated posteriorly with the usual seven spines on each side and the uropods beginning to show underneath (Figs. 1 *a*, *b*). The antennule (Fig. 1 *c*) shows on the outer branch three incipient segments, armed with two aesthetes and several hairs. The inner branch is represented by a long plumose seta. The antennal scale is not segmented at the tip; there is one seta externally and nine from the tip round the internal margin. The endopod is a long rod terminating in a setose spine, bearing on its external side about a third of the way up a long plumose seta (Fig. 1 *d*). The mandible, maxillule and maxilla are similar to those of the other species. The second and third maxillipedes bear five setae at the ends of the exopods, three at the tips. Rudiments of all the legs are present.

The essential differences between this larva and those of *S. occulta* and *S. cranchii*, as typical of the inshore species, are thus the long rostral spine and the form of the antennal endopod. Also the fact that it is larger and further advanced. There are no denticulations on the carapace which are usually, but not invariably, present in other species. The differences are of a character which would tend to make it better adapted for an open-water life. A comparison with the larvae of *Caridion gordoni* and *C. steveni* shows that these also have a long rostrum and a somewhat similarly shaped antenna. Gurney (1936) also has recently described the larva of *Latreutes fucorum* which has the antennal endopod of the same type. These are all Hippolytid larvae of the open water.

Miss Frost (1936) has described several larvae belonging to the genus *Spirontocaris* from Newfoundland waters, two of which have a long rostrum (*A* and *B*). Of these *A* has lateral spines on both abdominal segments 4 and 5, but *B* has them only on 5. It seems possible that *B* may be the later larva of *S. spinus*, for both *Spirontocaris spinus* and the var. *lilljeborgi* are recorded by Miss Rathbun (1929) from the Canadian Atlantic fauna.

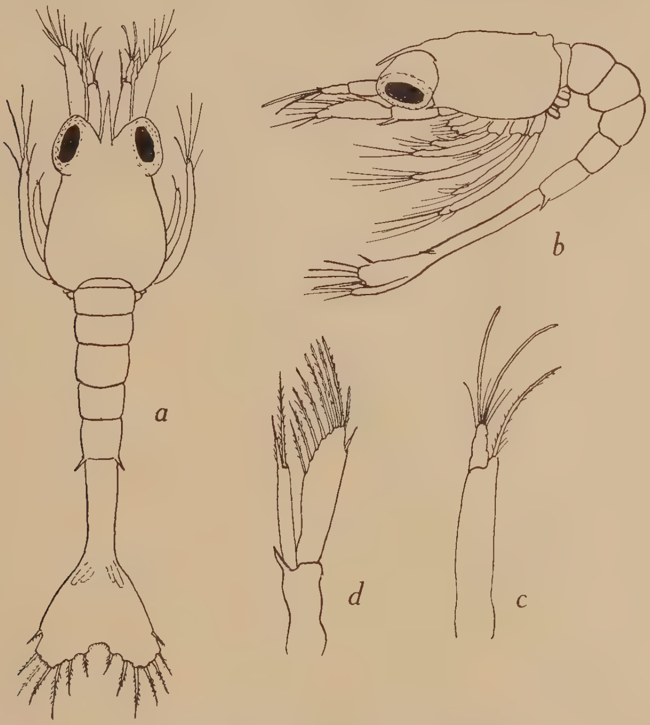


Fig. 1. *a*, dorsal view of newly-hatched larvae of *Spirontocaris spinus* var. *lilljeborgi*, 3·7 mm. long. *b*, the same, side view. *c*, antennule. *d*, antenna.

It is hoped that later larvae of *S. spinus* will be forthcoming, so that further comparison may be made, and that no opportunity of hatching the larvae of other species of the genus will be lost.

REFERENCES

Frost, N., 1936. Decapod larvae from Newfoundland waters. *Newfoundland Department of Natural Resources. Division of Fishery Research. Reports: Faunistic Series*, No. 1, pp. 11–24.

Gurney, R., 1936. Notes on some decapod Crustacea of Bermuda. I. The larvae of *Leptochela* and *Latreutes*. *Proc. Zool. Soc. London*, 1935, pp. 787–93.

KRØYER, H., 1842. Monografisk Fremstellung af Slaegten Hippolyte 's Nordiske Arter. *Ved. Sel. Naturvid. og Mathem. Afd.*, Deel IX, pp. 211–360.

LEBOUR, M. V., 1936. Notes on the Plymouth species of *Spirontocaris*. *Proc. Zool. Soc. London*, April, pp. 89–104.

NEEDLER, A. B., 1933. Larvae of some British Columbian Hippolytidae. *Contr. Canadian Biol. Fish.*, Vol. VIII, No. 18 (Series A, General, No. 39), pp. 239–42.

RATHBUN, M. J., 1929. *Canadian Atlantic Fauna.* 10. *Arthropoda.* 10 *m. Decapoda.* St Andrews, Canada.

SARS, G. O., 1912. Account of the post-embryonic development of *Hippolyte varians* Leach. *Archiv. f. Math. og Naturvid.* Vol. XXXII (1911), pp. 1–23.

STEPHENSEN, K., 1912. Report on the Malacostraca, Pycnogonida and some Entomostraca collected by the Denmark Expedition to North-East Greenland. *Danmark-Expedition til Groenlands Nordostkyst*, 1906–1908, Bind V, Nr. 11. *Medd. om Grønland*, XLV, pp. 503–630.

—— 1916. Zoogeographical investigations of certain fjords in Southern Greenland, with special reference to Crustacea, Pycnogonida, and Echinodermata. *Medd. om Grønland*, Vol. LIII, pp. 232–378.

—— 1935. Crustacea Decapoda. The Godthaab Expedition, 1928. *Medd. om Grønland*, Bd. 80, Nr. 1, pp. 1–94.

THE EGGS AND LARVAE OF THE BRITISH PROSOBRANCHS WITH SPECIAL REFERENCE TO THOSE LIVING IN THE PLANKTON

By Marie V. Lebour, D.Sc.
Naturalist at the Plymouth Laboratory

(Text-figs. 1–4)

CONTENTS

	PAGE
Introduction	105
Archaeogastropoda	110
Haliotidae	117
Fissurellidae	117
Patellidae	118
Lottiidae	119
Trochidae	119
Turbinidae	124
Mesogastropoda	124
Lacunidae	124
Hydrobiidae	128
Rissoidae	129
Tornidae	134
Skeneopsidae	135
Omalogyridae	135
Rissoellidae	135
Turritellidae	136
Caecidae	136
Cerithiidae	137
Cerithiopsidae	137
Mesogastropoda (*contd.*)	
Triphoridae	138
Epitoniidae	139
Ianthinidae	139
Eulimidae	140
Styliferidae	140
Pyramidellidae	141
Trichotropidae	142
Capulidae	143
Calyptraeidae	144
Aporrhaiidae	144
Naticidae	145
Lamellariidae	147
Cypraeidae	149
Stenoglossa	152
Muricidae	152
Buccinidae	154
Nassariidae	157
Turridae	158
References	162

INTRODUCTION

Molluscs are very important members of our marine fauna, and, since many of them are planktonic in their early stages, they contribute largely to the number of organisms available as food for plankton-eating animals. The present work includes the prosobranchs only, particularly those from Plymouth which have been specially studied during the last few years. Several papers have already been published dealing with the Plymouth species (Lebour, 1931–6), and these are referred to in due course. The present paper brings together the above work and that of others and summarizes our knowledge of the larval prosobranchs of Britain, with a description of the eggs. Naturally there are still many gaps, but it is hoped that these may be filled in time. A preliminary paper on the subject has already appeared (Lebour, 1933*f*). Closely related foreign species are referred to for comparison with our British forms. Original notes on certain species and information on the echinospira larva of *Capulus ungaricus* are given here for the first time. Figures of typical eggs and larvae are given.

Early work on the embryology of marine prosobranchs deals almost entirely with the development of the egg up to the time of hatching, and only in a few species, and these chiefly the primitive forms, is the larva described in the free-swimming stage. Very little was known about late veligers of the majority of the gastropods whose larvae remained long in the plankton. Lund's (1834) early classification of the various spawn cases is very interesting, although now out of date. Lamy (1928) gives a good account of the spawn of prosobranchs in general. Lovén (1839, 1844) and Krohn (1853, 1855, 1857) were some of the earliest workers to note prosobranch veligers in the plankton and to attribute them to their proper genera, and several planktonic larvae were described by others who believed them to be adult forms (*Sinusigera*, *Macgillivrayia*, etc.), although Macdonald (1855, 1859), Adams (1857, 1861) and Craven (1877, 1883) were already beginning to see their real significance. Fischer (1884) gives an account of these. These names are still sometimes used to denote larval forms whose adults are not known (Simroth, 1895; Vayssière, 1923–30). Simroth (1896, 1907, 1911), Fischer (1884), Odhner (1914), Pelseneer (1894, 1906, 1911, 1926) and recently Vestergaard (1935) all note various planktonic veligers, but of few if any were the complete life histories known. The recent exceedingly interesting work of Thorson (1935) on East Greenland prosobranchs shows that none in those regions has planktonic larvae but all hatch out in the crawling stage. Jeffreys (1863–69) notes the eggs and larvae of the British forms whenever possible. The very few planktonic larvae recorded by Simroth (1911) in his Gastropoda in *Nordisches Plankton* show the small number of free-swimming veligers known at that time from northern regions. Lo Bianco (1888–9) gives valuable notes on the breeding season and spawn of certain prosobranchs at Naples. Simroth (1896–1907) summarizes our knowledge of eggs and larvae with special reference to general embryology. General accounts are given by Pelseneer (1894, 1906), Fischer (1887) and MacBride (1914).

The study of the prosobranch gastropods at Plymouth indicates that a very large number live for a certain time as larvae in the plankton, including several species which live high up between tide marks. Those which remain only a few hours or days as veligers may yet be very important on account of their numbers or the long range of their breeding season. A few are of no importance at all from the point of view of plankton food, for they hatch out in the crawling stage, or, very rarely, are viviparous. As a rule the larvae with the most elaborate velum of four to six lobes (Fig. 4*c*, *g*, *h*) are those which are found farthest out to sea and remain longest in the plankton. These generally have a shell of several whorls before they settle down and lose the larval features.

Examples are *Nassarius incrassatus** and *Trivia arctica*, which both have a much larger velum with longer lobes than their close relatives *Nassarius reticulatus* and *Trivia monacha* to be found in shallower waters. Small forms may, however, have many whorls and an insignificant velum, and occur in even deeper water, remaining long in the plankton. Examples of such species are *Balcis alba*, *Triphora perversa* and *Cerithiopsis* spp., and some Turrids. These may, however, also be found in shallower waters.

To begin with the highest position on the shore, there are molluscs which usually live above high-water mark. Of these the classical instance is *Littorina saxatilis* (=*L. rudis*) which may be found beyond the highest tide limit and also between tide marks, and is viviparous. *L. neritoides*, formerly also regarded as viviparous, is now known to have planktonic egg capsules and to hatch out as a free-swimming veliger. This species has a restricted range and is generally to be found well above high-water mark, often with *L. saxatilis*. *Monodonta lineata*, one of the Trochidae, also living near high-water mark, sometimes with *Littorina neritoides*, sheds its eggs singly into the sea and so also does *Patella*, the common limpet. In both species a free-swimming larva results which remains a very short time in the plankton. The common species of *Gibbula*, *G. cinerarius* and *G. umbilicalis* have eggs and young similar to *Monodonta*. On the other hand, many of the Rissoids, living high up in the rock pools between tide marks, lay small capsules of eggs which hatch as veligers with a long free-swimming life. *Cingula cingillus* is a notable exception, for, living under stones sometimes above high-water mark, it lays egg capsules from which the young emerge in the crawling stage—and so also does *Cingula* (*Anoba*) *semicostata*, which lives rather lower down and is sometimes dredged below the low-water level. The position between tide marks or otherwise is not always the important factor in determining whether there is a free-swimming larval stage or a crawling young, for one Rissoid may live very high up and have a planktonic veliger, whilst another, closely related, may live much lower down and have no free-swimming stage at all. *Rissoa parva*, with an extensive range between tide marks, has a veliger which remains long in the plankton, whilst its close relative *Barleeia unifasciata*, which may be actually living with it at extreme low-water mark, has no free-swimming stage at all. *Littorina littoralis* (=*L. obtusata*) living on *Fucus* between tide marks has no free-swimming stage, the young hatching as miniatures of the parent; but *Littorina littorea*, often living quite near it on the rocks, has planktonic egg capsules with young hatching as veligers. Again, *Lacuna vincta* and *L. pallidula* both lay gelatinous masses of eggs on weeds between tide marks, but the first has free-swimming larvae, while the latter hatches in the crawling stage. Many of the Stenoglossa, either living between tide marks or always under water, hatch in the crawling stage (*Buccinum undatum*, *Nucella lapillus*, etc.), but may have free-swimming larvae, for example, all the British Turrids whose larvae are known. From these few instances one sees that on British coasts it is usually impossible to deduce from the habitat of the mollusc what sort of larva it will have. Each species must be studied separately and its life history known before we can be sure which is important in the plankton and which is not.

---

* The nomenclature is according to Winckworth's list (1932). When this differs from the Plymouth Marine Fauna (Marine Biological Association, 1931) the equivalent names are placed in brackets.

The prosobranchiate gastropods are divided into three orders, the Archaeogastropoda, the Mesogastropoda and the Stenoglossa. Of these the Archaeogastropoda are clearly differentiated from the other two in the larval form, the young being of a much more primitive character. The embryology of this order has been investigated much more thoroughly than that of the other two, and a fair amount is known of the eggs and young and their development. There is frequently a free-swimming trochophore stage, and the velum is a flat organ with a more or less circular outline. The nourishing material is contained in the egg itself as in *Patella* and *Patina*, or there is a thin layer round the egg membrane as in *Gibbula* and *Monodonta*. In consequence the nourishment available is small and the planktonic stage is short; nevertheless, in the common shore species, *Patella*, *Gibbula*, etc., the larvae are so numerous that they are very important members of the plankton. *Diodora*, *Calliostoma* and *Cantharidus* hatch in the crawling stage.

In the Mesogastropoda and Stenoglossa the eggs are not shed singly into the water, but, unless the animal is viviparous, they are covered with a more or less thick protective sheath or capsule. The larva is nourished inside this until it escapes either as a well-formed veliger with a bilobed or four-lobed velum or as a crawling form resembling its parent. Usually the more safely the eggs are protected the fewer there are in the sheath or capsule.

The eggs and simple free-swimming early larvae of the Archaeogastropoda before the shell is formed are all very much alike, but there is a great variety both in the spawn and larva of the other two orders.

THE EGG AND ITS COVERING

(Figs. 1 *a*, *b*, *c*, *g*, *k*, *l*, *m*)

When newly extruded from the ovary the egg (*E*) is provided with a thin membrane—the egg membrane (*M*). A thin gelatinous layer sometimes covers this, as in *Patella* (Fig. 1 *c*, *G*) and *Patina*, which swells up in the water. The membrane and gelatinous layer very soon disappear in *Patella* and its relatives and development of the egg proceeds without any covering. In most of the Archaeogastropoda, however, the egg membrane is covered by an albuminous layer (*A*), more or less thin, and an outer coat, the egg covering (*C*), a gelatinous sheath which swells up in the water frequently covering the whole (*G*). The egg covering is called by some authors the egg capsule, the latter term being here reserved for the hardened outer sheath which is outside the covering and

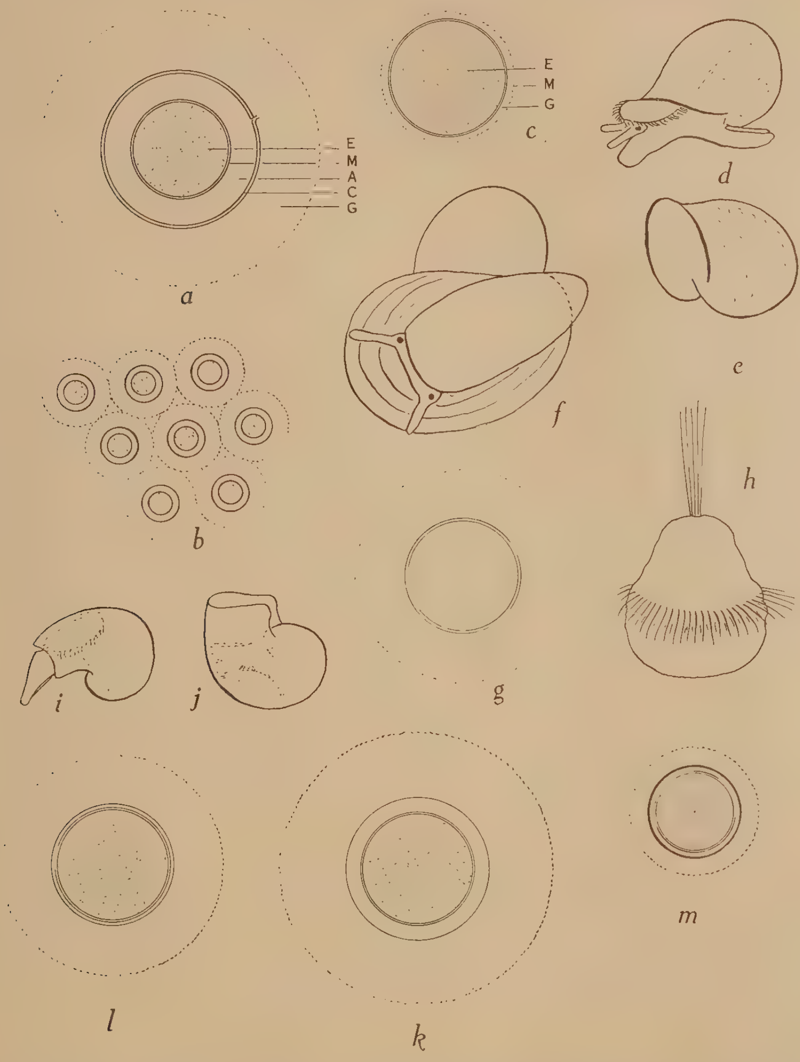


Fig. 1. *a, b*: *Diŏdora apertura*. *a*, individual egg, 0·48 mm. across gelatinous layer; *b*, eggs from egg mass. *c–f*: *Patella vulgata*. *c*, egg, newly laid, 0·16 mm. across; *d*, crawling larva with velum, shell 0·2 mm. across; *e*, shell of same; *f*, young shell from rock crevice, 0·38 mm. across. *g–j*: *Patina pellucida*. *g*, egg, newly laid, 0·32 mm. across; *h*, trochopore larva 0·2 mm. high; *i* and *j*, veligers, with shells 0·16 mm. and 0·18 mm. across. *k*: *Monodonta lineata*, egg, 0·48 mm. across. *l*: *Gibbula umbilicalis*, egg, 0·32 mm. across. *m*: *Tricolia pullus*, egg, 0·14 mm. across.

occurs mainly in the higher prosobranchs. Single eggs with membrane, albuminous layer, egg covering and gelatinous sheath occur in *Gibbula*, *Monodonta* and *Tricolia* (Fig. 1 *k*, *l*, *m*). In *Diodora* (Fig. 1 *a*, *b*) the gelatinous sheath of each egg joins its neighbour, so that a layer of eggs, one cell thick, is laid on a substratum. This leads to the gelatinous ribbon of many of the Trochidae—*Calliostoma* and *Cantharidus*—in which a further gelatinous substance keeps the mass of eggs together (Fig. 2*a*). This gelatinous substance may form a pellicle on the outer surface, making the egg mass or ribbon more or less firm. So far as is at present known no more elaborate form of spawn occurs in the Archaeogastropoda.

In the Mesogastropoda and Stenoglossa the outer covering may be soft or hard and frequently forms a capsule of very definite shape—lens-shaped, flask-shaped, vase-shaped, etc. The various layers covering the eggs are formed from special glands, different according to the kind of spawn. These are well described for *Littorina* by Linke (1933*a*) and for *Lacuna* by Hertling (1928). Pelseneer (1910, 1926) has also described some of these glands and gives a further list of authorities. In the Mesogastropoda and Stenoglossa the egg membrane is often very difficult to see, but is probably always present at some time. Frequently the egg is without a perceptible membrane and floats in a nourishing fluid contained in the capsule (*Rissoa*, *Nassarius*) or it may be covered with an albuminous layer and egg covering and then float in the capsule (*Littorina littorea*). In *Littorina littorea* the outer capsule contains a fluid in which float one to five eggs, each with an egg membrane, an albuminous layer and an egg covering, whilst in *Rissoa* the egg or eggs, covered by a very thin membrane, float directly in the fluid contained in the capsule.

In the following lists the various kinds of eggs and larvae are roughly grouped together, so far as they are known. Under the Archaeogastropoda and Stenoglossa both are treated together, but they are dealt with separately under the Mesogastropoda.

ARCHAEOGASTROPODA

Eggs set free singly in the plankton, veliger stage short. Larvae of some importance in the plankton (Fig. 1 *c*, *g*, *k*, *l*, *m*):

Haliotis tuberculata
Patella vulgata (and allied species)
Patina pellucida
Patelloida virginea
Gibbula magus
Gibbula cineraria
G. umbilicalis
Monodonta lineata
Tricolia pullus

Eggs laid in gelatinous masses or ribbons, young hatched in crawling stage. Larvae of no importance in the plankton (Figs. 1 *a*, *b*; 2 *a*):

Diodora apertura
Gibbula tumida
Margarites helicinus
Calliostoma zizyphinum
Calliostoma papillosum
Cantharidus striatus
C. exasperatus
Skenea serpuloides

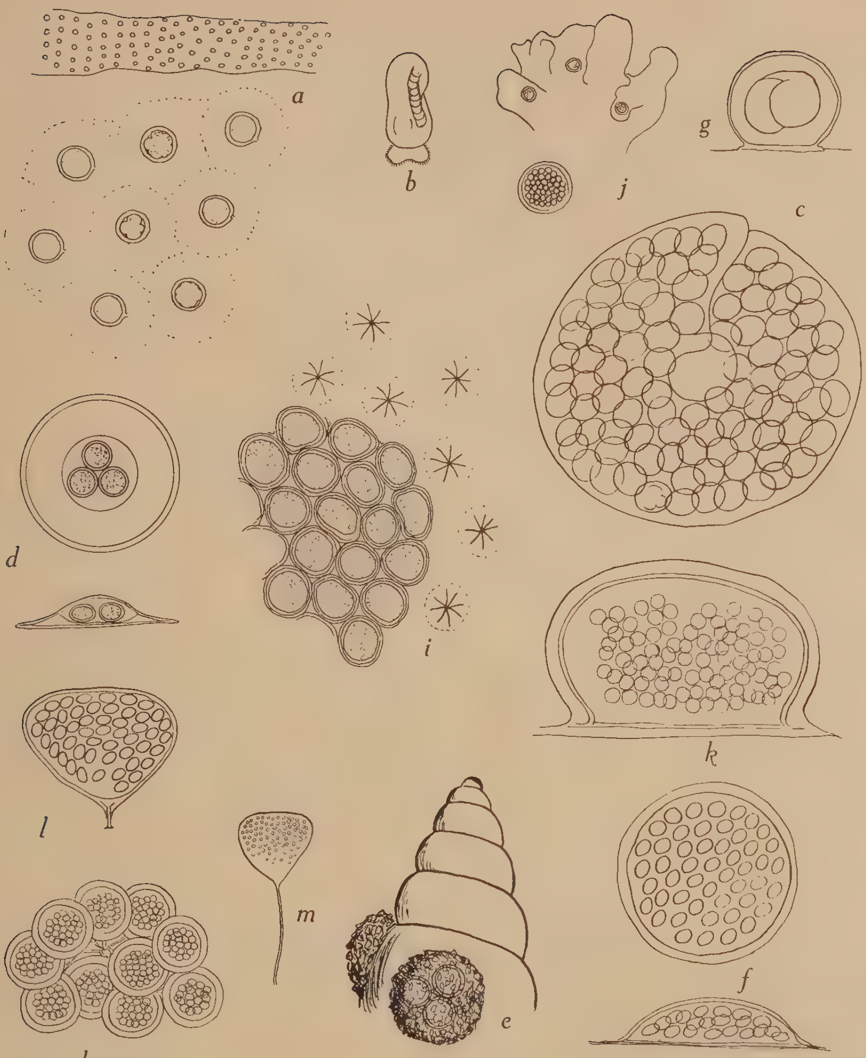


Fig. 2. *a*: *Calliostoma zizyphinum*, eggs 0·32–0·4 mm.; portion of egg ribbon and a part more highly magnified. *b*: *Omalogyra atomus*, with eggs inside shell. *c*: *Lacuna vincta*, egg mass, 3 mm. across. *d*: *Littorina littorea*, planktonic egg capsule, 0·96 mm. across. *e*: *Hydrobia ulvae*, egg capsule laid on neighbour's shell, *ca.* 0·6 mm. across. *f*: *Rissoa parva*, egg capsule, 0·64 mm. across. *g*: *Skeneopsis planorbis*, egg capsule, 0·48 mm. across. *h*: *Turritella communis*, egg capsules; capsule 0·64 mm. across. *i*: *Simnia patula*, egg capsules; capsule 0·13 mm. across. *j*: *Cerithiopsis tubercularis*, egg capsules laid in the sponge *Hymeniacidon*; capsule 0·35 mm. across. *k*: *Balcis alba*, egg capsule, 3 mm. across. *l*: *Pelseneeria stylifera*, egg capsule, 1·2 mm. across. *m*: *Crepidula fornicata*, egg capsule, 3·5 mm. across (from mass covered by parent).

MESOGASTROPODA

VIVIPAROUS

Littorina saxatilis
Hydrobia ventrosa (fresh water, near sea)

LAYING EGGS

Eggs in capsules carried inside shell:

Omalogyra atomus (Fig. 2*b*)

Eggs in gelatinous masses attached to a substratum:

Littorina littoralis
Lacuna vincta (Fig. 2*c*)
Lacuna pallidula
Odostomia eulimoides

Eggs in planktonic capsules:

Littorina littorea (Fig. 2*d*)
L. neritoides
Several unknown species

Eggs in lens-shaped capsules attached to the substratum containing several eggs:

Hydrobia ulvae (laid on shell of neighbours) (Fig. 2*e*)
Cingula semistriata
Alvania punctura
Rissoa sarsii
Rissoa inconspicua
R. parva (Fig. 2*f*)
R. guerini
R. membranacea
Chrysallida decussata

Eggs in spherical or oval capsules containing one or two eggs, attached to substratum or on bottom:

Cingula fulgida
C. semicostata
C. cingillus
Barleeia unifasciata
Skeneopsis planorbis (Fig. 2*g*)
Rissoella diaphana
Aporrhais pespelicani

Eggs on bottom in grape-like clusters:

Turritella communis (Fig. 2*h*)

Eggs in layers of capsules, one cell thick or one capsule thick, on a substratum:

Triphora perversa
Simnia patula (Fig. 2*i*)

Eggs in nests in sponges:

Cerithiopsis tubercularis (Fig. 2*j*)
Cerithiopsis barleei

Eggs in attached gelatinous coils:

Bittium reticulatum

Eggs in thick, tough, oval capsules attached to a substratum:

Balcis alba (Fig. 2*k*)

Eggs in triangular capsules attached to echinoderm:

Pelseneeria stylifera (Fig. 2*l*)

Eggs in capsules covered by parent shell:

Calyptraea chinenis
Capulus ungaricus
Crepidula fornicata (Fig. 2*m*)

Eggs in vase-shaped or circular capsules embedded in compound ascidian:

Trivia monacha (Fig. 3*a*, *b*) and (almost certainly) *T. arctica*
Lamellaria perspicua

Eggs glued in ribbons of sand:

Natica catena
Natica poliana (Fig. 3*c*)

Eggs in chains of triangular or polygonal capsules covered with sand or mud:

Clathrus clathrus (Figs. 3*d*, *e*)

LARVAL FORMS

Young hatched in the crawling stage. Of no importance in the plankton:

Littorina littoralis
Lacuna pallidula
Cingula cingullus
C. fulgida
C. semicostata
Barleeia unifasciata
Skeneopsis planorbis
Rissoella diaphana
Calyptraea chinensis

Larvae hatched as veligers with a short free-swimming stage. Of little importance in the plankton:

Hydrobia ulvae
Rissoa membranacea
Turritella communis

Larvae hatched as veligers with a long larval life. Of importance in the plankton:

Littorina littorea
Rissoa sarsii
R. parva
R. guerini
R. incospicua
Cingula semistriata
Alvania punctura
A. crassa
Tornus subcarinatus
Caecum imperforatum
Odostomia eulimoides
Aporrhais pespelicani
Triphora perversa
Cerithiopsis tubercularis
C. barleei
Bittium reticulatum
Balcis alba
B. devians
Pelseneeria stylifera
Lamellaria perspicua
(?) *L. latens*
Capulus ungaricus
Velutina velutina
Trivia monacha
T. arctica
Erato voluta
} echinospira larvae (Figs. 4*a*–*d*)
Simnia patula
(?) *Natica catena*
(?) *N. poliana*

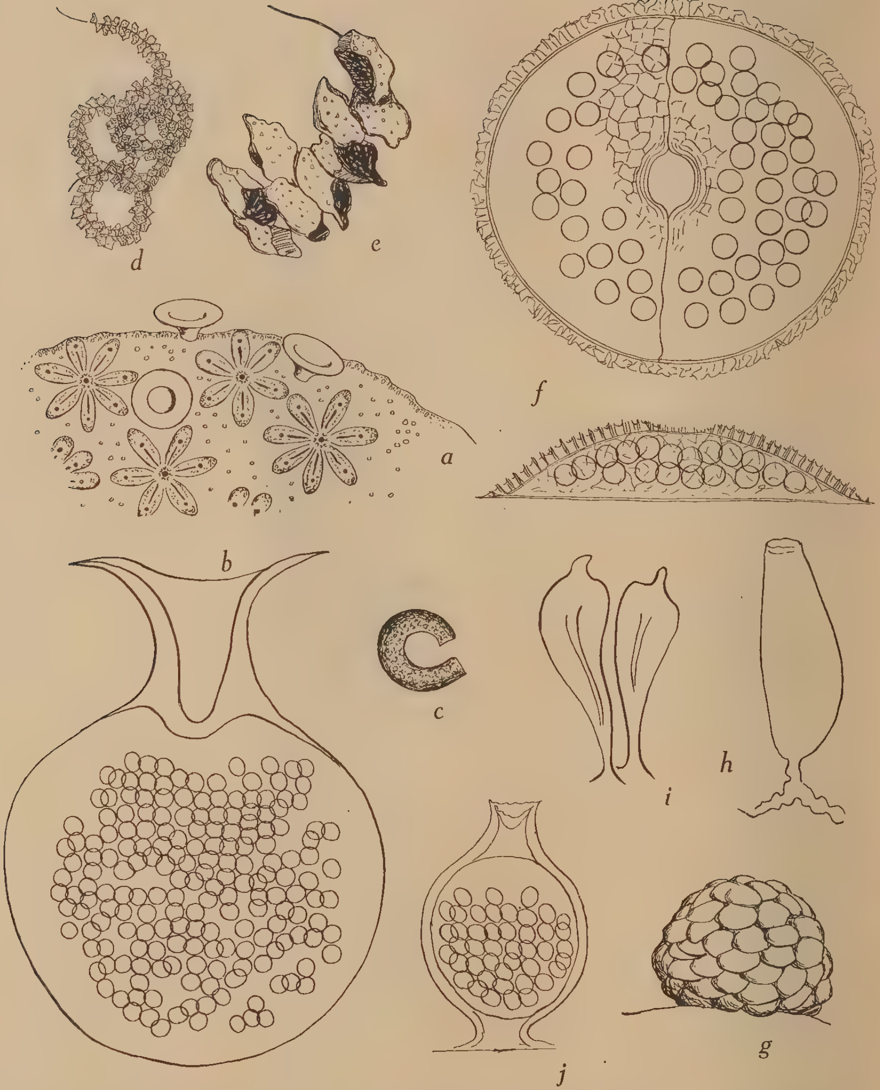


Fig. 3. *a*, *b*: *Trivia monacha*. *a*, egg capsules in compound ascidian; *b*, a capsule of same isolated, 4·8 mm. high. *c*: *Natica poliana*, egg ribbon, *ca.* 25 mm. across. *d*, *e*: *Clathrus clathrus*. *d*, egg chain, *ca.* 60 mm. across. *e*, part of same highly magnified, capsule, *ca.* 3 mm. long. *f*: *Philbertia gracilis*, egg capsule, 3·4 mm. across. *g*: *Buccinum undatum*, egg mass, *ca.* 80 mm. across. *h*: *Nucella lapillus*, egg capsule, 8 mm. high. *i*: *Ocenebra erinacea*, egg capsule, 10 mm. high. *j*: *Nassarius incrassatus*, egg capsule, 2 mm. high.

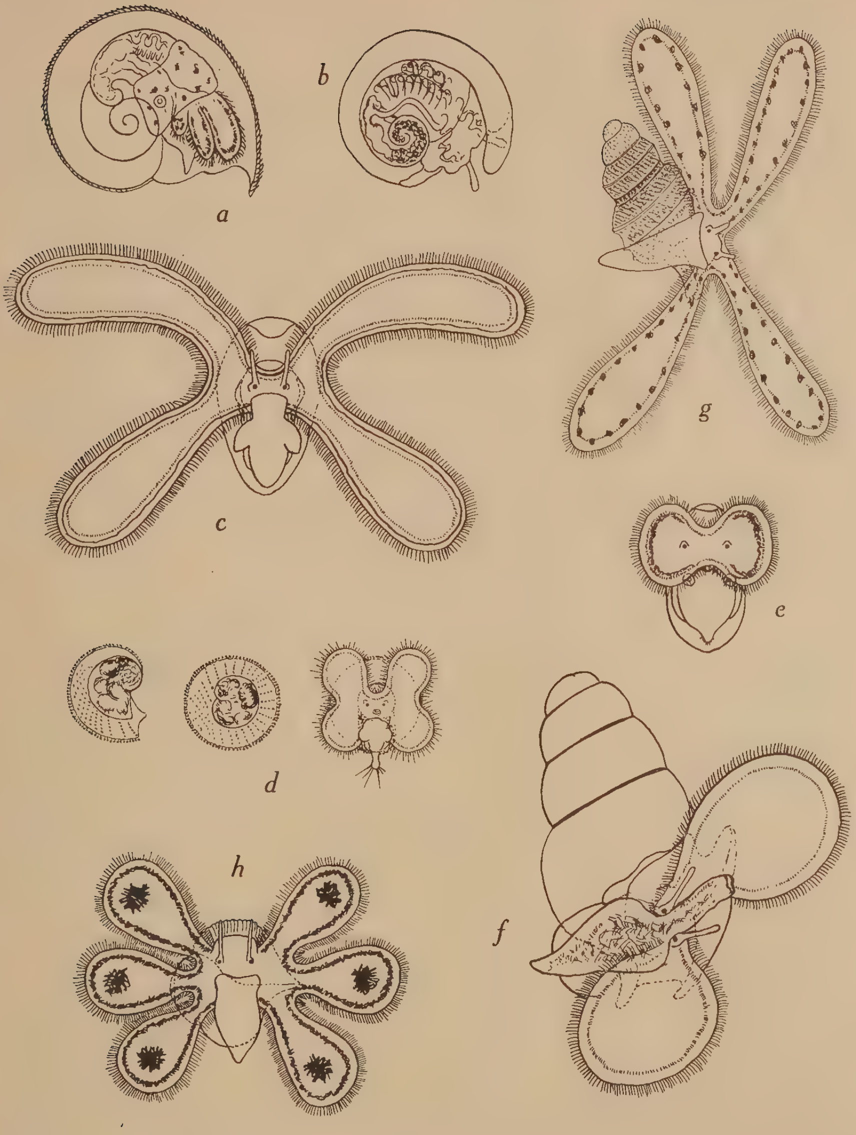


Fig. 4. *a*: *Lamellaria perspicua*, echinospira larva, 2·24 mm. across (nautiloid form). *b*, *c*: *Trivia arctica*. *b*, echinospira larva, 1·44 mm. across (helicoid form). *c*, echinospira larva with velum expanded. *d*: *Capulus ungaricus*, echinospira larva. *e*: *Lacuna vincta*, newly hatched veliger, velum two-lobed. *f*: *Cerithiopsis tubercularis*, late veliger; typical late larva with two-lobed velum. *g*: *Philbertia gracilis*, late veliger, typical four-lobed velum. *h*: *Aporrhais pespelicani*, late veliger, typical six-lobed velum.

STENOGLOSSA

Separate attached lens-shaped capsules containing several eggs. Young hatched in the crawling stage. Of no importance in the plankton:

Trophon muricatus

Lens-shaped capsules attached to a substratum, containing several eggs. Free-swimming larvae remaining long in the plankton. Of importance in the plankton:

Lora turricula
Mangelia nebula
Philbertia gracilis (Figs. 3*f*; 4*g*)
Philbertia leufroyi
P. linearis

Eggs in more or less lens-shaped capsules, congregated together in lumpy masses, young hatched in crawling stage. Of no importance in the plankton:

Buccinum undatum (Fig. 3*g*)
B. humphreysianum
Neptunea antiqua

Eggs in solitary capsules, or a few capsules together. Young hatched in crawling stage. Of no importance in the plankton:

Beringius turtoni
Volutopsius norwegicus
Colus islandicus
Colus gracilis
C. howsei

Eggs in vase-shaped capsules, usually several together, attached to a substratum, containing several eggs. Young hatched in crawling stage. Of no importance in the plankton:

Nucella lapillus (Fig. 3*h*)
Ocenebra erinacea (Fig. 3*i*)
Urosalpinx cinerea

Eggs in flask-shaped capsules, attached to a substratum, containing several eggs. Free-swimming larvae remaining long in the plankton. Of importance in the plankton:

Nassarius reticulatus
N. incrassatus (Fig. 3*j*)
Nassarius pygmaeus

Order ARCHAEOGASTROPODA

(Figs. 1*a–m*; 2*a*, *b*)

The eggs are laid singly in the water, hatching as trochophore larvae, or in a layer, mass, or ribbon, attached wholly or partly to a substratum and hatching in the crawling stage, the trochophore stage being passed within the egg covering. The velum is circular or (rarely) beginning to be bilobed.

The embryology of this order has been worked out in several genera and species (Boutan, 1885, 1898, 1899; Patten, 1886; Robert, 1902; Smith, 1935; etc.), although less has been done with the later larval stages and post-larval than with the early stages.

Family HALIOTIDAE

Genus Haliotis

Haliotis tuberculata L.

The "Ormer" occurs commonly in the Channel Islands but not on the British mainland. Boutan (1885, 1899) describes the eggs, which are set free singly from the holes along the shell. Each egg is a small sphere enveloped in a covering, 0·2 mm. in diameter, surrounded by a little mucus; the yolk is dark green. Wegmann (1884) also describes the egg. Later work on egg and young is by Stephenson (1924) who obtained trochophores 14–15 hours after fertilization, the larvae hatching from the egg shell (= egg covering) after 44–46 hours. Boutan figures the young larvae and shell, the round velum, the crawling stage and the adult shell beginning to form. The larval shell is at first a single cup, then nautiloid, and finally spiral with about one and a half whorls. The larval operculum disappears at the same time as the velum. At first the shell is without holes, which begin to appear when the animal is less than 1 mm. long. The free-swimming stage is very short. Crofts (1929) gives a brief review of the eggs and larvae. She found young, 2 mm. long, crawling on stones.*

Family FISSURELLIDAE

Genus Diodora

Diodora apertura (Montagu) (Figs. 1 *a*, *b*).

Common in many parts of Britain among rocks near the shore. The eggs are laid in layers one cell thick under stones. Boutan (1885) gives a detailed account of the embryology from the expulsion of the eggs until the fully formed shell stage. The eggs are extruded from the branchial aperture and are apparently fertilized externally. The young hatch in the crawling stage, the velum having almost entirely disappeared. The shell of newly hatched young is spiral, with about one and a half whorls. Later a slit appears at the edge of the older shell, which as the animal and shell grow is gradually closed up and finally reaches the top of the shell.

A male and female were placed in a glass bowl in the Plymouth Laboratory (May 1934), and eggs were laid in an extensive layer, several inches across, on the glass. These agreed with the description of Boutan. The eggs were 0·14 mm. across the thin membrane, yellowish and very opaque, surrounded by an albuminous layer and an egg covering with a micropyle. Round this was a thick gelatinous layer, the whole being about 0·48 mm. across. The gelatinous coverings were pressed together and formed a layer one cell thick, the whole mass measuring about 2½ in. across. The developing young rotated in the egg covering and grew as far as the ciliated stage, the membrane disappearing. Breeding records from Plymouth are in the months of December, January, March and May.

Lo Bianco (1899) found similar eggs belonging to a related Mediterranean species (*Fissurella nubecula* L.).

---

* See note on page 166.

Family PATELLIDAE

(Figs. 1*c–j*)

All the members of this family whose breeding is known extrude the eggs singly and fertilization is external. The egg is surrounded by a thin membrane and a gelatinous layer, more or less thick, which swells up in the water. Both disappear soon and development proceeds without any covering. The larva hatches in a few hours as a trochophore with long cilia at the top and a circle of cilia surrounding it. Very soon a simple bowl-shaped shell is developed, and a circular velum, tentacles, eyes and otocysts and an operculum are formed. The shell rapidly becomes slightly spiral with hardly more than one whorl and soon the larva can both swim and crawl. After this it loses the velum and operculum, having only been a few days in the plankton, and settles down, a secondary symmetry appearing both in the shell and the animal.

Patten (1886) describes the embryology of *Patella cerulea*, and Lo Bianco (1899) reared the same species at Naples from artificial fertilizations. Wilson (1904) worked experimentally on the egg. Boutan (1899) describes briefly the embryology of *Patella vulgata*. Ainsworth Davis and Fleure (1903) give a short account of its development and so also does Pelseneer (1911). F. G. W. Smith (1935) describes its development from the egg to the settling stage in detail.

Patina pellucida was found by Smith and also by myself to have eggs and young larvae somewhat similar to *Patella*, but the larvae are distinguishable. The free-swimming larvae of this family, although staying only a short time in the plankton, are yet of importance on account of their abundance.

Genus Patella

Patella vulgata L. (Figs. 1*c–f*).

This is the species most commonly studied in Britain, but the allied *P. depressa* (including *P. athletica*) and *P. intermedia* have been probably confused with it. It is likely, however, that most of the work by British zoologists is on *P. vulgata* and this is certainly so with Smith's work (1935). This species breeds at Plymouth chiefly during the winter months, but the breeding records may refer to any of the common species referred to above. Orton (1928) found it bred from August to March at Plymouth, the maximum season being in January and February. In March Professor Ohshima reared *P. vulgata* through metamorphosis to young spat from artificial fertilizations (Orton, 1928), and MacBride (1914) states, probably alluding to unpublished work by the late E. W. Nelson, that it was reared at Plymouth through metamorphosis. This has again been accomplished by Smith (1935).

The newly extruded egg is 0·16 mm. across (Fig. 1*c*). The young developing larva is about 0·16 mm. across and the trochophore about 0·18 mm. across. The young shelled larva is 0·2 mm. across. In the late larva, which can both crawl and swim, the shell is 0·22 mm. across. The shell has minute granulations (Fig. 1*d*, *e*). The shelled larvae a few days old can be found in numbers in tow-nettings from Plymouth Sound in autumn and winter, especially in January and February, more rarely in late spring and summer. They then settle down and are to be found in barnacle shells and small rock crevices (Fig. 1*f*).

Genus Patina

Patina pellucida (L.) (Figs. 1*g*–*j*).

The egg has an egg covering and a thin gelatinous layer rather thicker than in *Patella*, both of which soon disappear (Fig. 1*g*). Artificial fertilizations were effected at Plymouth and the larvae reared by Smith (1935), and to early stages by myself. The larva is like *Patella*, at first a trochophore (Fig. 1*h*), then with velum and shell. The shells differ from those of *Patella* in being smaller, smooth and more symmetrical at the outer lip, the margin overlapping at both sides (Figs. 1*i*, *j*). The egg is 0·32 mm. across the gelatinous covering; the newly hatched larva 0·2 mm. high; the shell of the late larva 0·16–0·18 mm. across. The species probably breeds at Plymouth throughout the year; the shelled larvae are to be found in the plankton in almost any month and sometimes occur in numbers.

Family LOTTIIDAE

Genus Patelloida

Subgenus *Collisella*

Patelloida tessullata (Müller).

This species lays its eggs embedded in a layer of very thin mucus in which they lie one layer deep at regular distances; the eggs are not shed singly into the water. A trochophore larvae is developed very rapidly (Willcox, 1905).

Subgenus *Tectura*

Patelloida virginea (Müller).

Boutan (1898, 1899) has described the development as very similar to *Patella*.

In the closely related *Acmaea rubella*, Thorson (1935) has shown the existence of viviparity.

Family TROCHIDAE

(Figs. 1*k*, *l*, *m*; 2*a*, *b*)

The members of this family, so far as is known, either shed their eggs singly into the sea, like *Patella*, or they deposit them in gelatinous masses or ribbons attached partly or wholly to some substratum. Robert (1902) has described the eggs and embryology of several British species and some others in his classical monograph. This work gives us the most important information which we possess on the eggs and young of the family. Gersch (1936) describes the spawn of some of the species in his detailed account of the genital organs. Moorhouse (1932) states that the large *Trochus niloticus*, economically important in Australian regions, sends out its eggs separately into the sea where they float in the surface layers. He describes the newly extruded egg as spherical with a diameter ("chorion" included) of 0·3 mm., the egg proper being 0·17–0·25 mm. across. This kind of egg is typical of certain members of the family, notably various species of *Gibbula* and *Monodonta lineata*.

The egg (Figs. 1 *k*, *l*, *m*), covered by a thin membrane, lies in an egg covering with a more or less thick albuminous layer between. A micropyle is usually to be seen in the egg covering. Outside the covering is a gelatinous layer which swells up in the water. The single eggs float separately in their spheres of jelly. In most of those species which lay masses or ribbons of eggs the gelatinous spheres are embedded in a further coating of a glutinous nature, which fixes the eggs together and serves as an attachment to some substratum (Fig. 2*a*). They have thus gone a step farther than the Fissurellidae.

When the eggs are laid singly the young are hatched in an early trochophore stage, not unlike that of *Patella*; but the membrane, albuminous layer and egg covering with the gelatinous sheath are retained for some time and the larva can be seen revolving inside its coverings. Later, after hatching, a shell and round velum are formed. The larva remains only a few days in the plankton. Before settling down the shell is already spiral.

In those species which lay their eggs in masses or ribbons the larvae, so far as is known, are hatched in the crawling stage, having passed the veliger stage within the egg covering. Known species of *Calliostoma* have the ribbon attached at one end or for part or the whole of one surface, in those of *Cantharidus* the eggs are in smaller masses attached by the whole of one surface. The eggs may be arranged irregularly or in a chaplet. Here again, although only remaining for a short time in the plankton, those larvae which are free-swimming are of importance on account of their abundance.

Winckworth (1932) places the genus *Gibbula* after *Calliostoma*; but from the nature of the spawn it is more closely related to *Patella* and probably should hold the first place among the Trochidae, *Monodonta* following it. A more natural sequence seems to be Trochidae: *Gibbula*, *Monodonta*, *Margarites*, *Calliostoma*, *Cantharidus*. The fact that Gersch (1936) has found that *Gibbula tumida* lays egg masses intermediate between the free eggs and those in gelatinous ribbons or masses shows that it should be placed probably between *Monodonta* and *Margarites*. The genera are, however, here left in the order in which they appear in Winckworth's list.

Genus Margarites

Margarites helicinus (Fab.).

Jeffreys (1867, III, p. 297) states that the spawn is deposited on seaweed and the under sides of stones. Each egg is enclosed in a yellow membranous capsule, the capsules agglutinated together at the sides to form an irregular "glairy" mass. Thorson (1935, p. 62, figs. 69, 70) has found the egg masses (almost certainly of this species) in East Greenland, and describes them and the young stages. The egg masses are small slimy lumps, each containing about 100–200 irregularly arranged eggs, attached to *Laminaria* or *Fucus* fronds. From the lump there emerge several slimy strings which help to fasten the egg masses to the substratum. The eggs are yellowish white. The veliger stage is passed within the capsule and the young emerge in the crawling stage with a shell of one and a fourth whorls (basal diameter *ca.* 0·25 mm.).

Margarites groenlandicus (Gmelin).

Thorson (1935, p. 63, fig. 70) assumes that this species lays similar egg masses to those of *M. helicinus*, and has a direct development. The embryonic whorls are exactly similar to those of that species and they are difficult to separate in the young stages.

Genus Calliostoma

The eggs in both the species in which they are known are laid in long gelatinous ribbons, attached more or less firmly, usually by one end, to some substratum, and partly floating. The young are hatched in the crawling stage.

Calliostoma zizyphinum (L.) (Fig. 2*a*).

Robert (1902, p. 286) describes the spawn and young of *Trochus conuloides*, subgenus *Zizyphinum* (= *Calliostoma zizyphinum*) and figures the newly hatched larva. Lebour (1936, p. 547, pl. i, figs. 1–5) describes the eggs and young. The egg ribbon is many times longer than broad containing hundreds of eggs, attached by one end and floating. The egg is about 0·28 mm. across the egg covering when newly laid. In the newly hatched young there are about one and a half whorls, deeply pitted with large polygonal areas; longitudinal striations following even before hatching. The diameter of newly hatched shells is 0·32 mm. Jeffreys (1867, III, p. 332) describes the "fry" as slightly umbilicate with the topmost whorls reticulate. The breeding season is in spring and summer.

Calliostoma papillosum (da Costa).

This is the *Trochus granulatus* Born of Jeffreys. Robert (1902, p. 285), who saw the eggs laid, states that this species spawns at Roscoff throughout the year. The spawn is like that of *C. zizyphinum*, floating and attached loosely at three points. The eggs are yellow and numerous, 0·17 mm. across, and irregularly arranged, resembling those of *C. zizyphinum*. Jeffreys (1867, III, p. 329) states that the first whorl is smooth, the second regularly and strongly cancellated, with a conspicuous umbilicus.

Genus Gibbula

The eggs are shed singly into the water, hatching as trochophores and attaining a shell before settling down. *Gibbula tumida*, which is shown by Gersch (1936) to lay its eggs in irregular gelatinous masses, should probably be placed in another genus.

Gibbula eggs are common in the Plymouth plankton, especially in autumn and spring, and although free-swimming for so short a time must be important on account of their numbers.

Gibbula magus (L.).

Robert (1902, p. 288) describes eggs and young from Roscoff. The eggs are yellowish, 0·12 mm. across, with a gelatinous covering much swollen in the water. The young hatch in about 20 hours as trochophores. The shell appears in a few hours, and is at first simple, then spiral. In 150 hours tentacles, eyes and epipodial tentacles were present. Jeffreys (III, p. 307) describes the very young shells as being equally convex on each side of the peripheral keel and with the umbilicus very small.

Gibbula tumida (Montagu).

Jeffreys (III, p. 309) states that the "fry" are often marked with spiral pink lines. Gersch (1936) describes and figures the spawn, which is laid in irregular gelatinous masses, much simpler than those of *Calliostoma*, the gelatinous material probably corresponding to the external coating in that genus. The eggs are 140μ across. Judging from the form of the spawn this species, as suggested above, should probably be placed in a different genus.

Gibbula cineraria (L.).

Robert (1902, p. 288) states that this species breeds at Roscoff in June. Eggs like those of *G. magus*, developing and hatching in the same way. At Plymouth ripe eggs may be found in the females in almost any month. Jeffreys (III, p. 312) states that the "fry" are not angulated at the base.

Gibbula umbilicalis (da Costa) (Fig. 1*l*).

Robert (1902, pp. 6, 17), who refers to the species as *G. obliquatus*, states that the eggs are similar to those of *G. magus* and *G. cineraria*. Eggs taken from a female at Plymouth were 0·2 mm. across the egg covering, the egg itself being about 0·15 mm. across. The species breeds near Plymouth throughout the year, but especially in winter. Jeffreys (III, p. 315) describes the "fry" as white, nearly flat, with only two or three permanent ribs. A young shell from Plymouth with only a few whorls was beautifully marked with thick rose-pink longitudinal lines and was conspicuously striated spirally. Judging from the embryonic whorls of this specimen the free-swimming young must be exceedingly small.

Genus Cantharidus

The eggs are laid in small gelatinous masses attached by the whole of one surface. The young are hatched in the crawling stage.

Subgenus *Jujubinus*

Cantharidus exasperatus (Pennant).

Robert (1902, p. 288) describes the spawn as being like that of *C. striatus* (as *Trochus*, subgenus *Zizyphinus*), breeding at Roscoff in spring and summer. The eggs are laid in chaplet form in an ovoid gelatinous mass, flat and fixed by one surface; they are uncoloured. The egg is 0·16 mm. across, like that of *Calliostoma zizyphinum*. The young go through the veliger stage within the egg covering and hatch in the crawling stage. Jeffreys (III, p. 325) states that the "fry" can be distinguished from those of *striatus* and exhibit the same relative characters as the adult.

Cantharidus striatus (L.).

Robert (1902, p. 230) made a special study of this species (as *Trochus*, subgenus *Zizyphinus*). It lays its eggs in gelatinous oval masses on weeds and stones in large quantities, 20–40 mm. long and 1·15 mm. broad, solidly fixed by one of its large surfaces. The eggs are in the form of a chaplet, whitish and disposed in a flattened spiral. The egg is 0·16 mm. across, much like that of *C. exasperatus*, and hatches in the crawling stage. The veliger is complete in 22 hours. The young are hatched in 124 hours, having already epipodial tentacles. The species breeds almost throughout the year at Banyuls and Roscoff.

Cantharidus montagui (W. Wood).

Jeffreys (III, p. 322) states that the spiral ridges of the "fry" are frequently marked with reddish lines.

Subgenus *Clelondella*

Cantharidus clelondi (Wood).

This species is the *Trochus* (*zizyphinus*) *milligranus* of Jeffreys who states (III, p. 326) that the "fry" has an umbilical perforation.

Genus Monodonta

Subgenus *Osilinus*

Monodonta lineata (da Costa) (Fig. 1 *k*).

Robert (1902, p. 294) states that the absence of a special gland suggests that the egg laying is similar to that of *Gibbula*. This is borne out in specimens from

Plymouth in which ripe eggs, found in March and April, were very like those of *Gibbula*. Placed in sea water the eggs have a wide spherical gelatinous covering outside the egg covering. The egg is 0·16 mm. across, and the gelatinous covering 0·29 mm. across.

Genus Skenea

Skenea serpuloides (Montagu).

Jeffreys (III, p. 291, as *Cyclostrema*) states that this species deposits its spawn in thick irregular clusters on some of the finer and more membranous seaweeds. Each cluster contains a great number of "fry", having their shells completely formed and enveloped in a "glairy" mass.

Family TURBINIDAE

Genus Tricolia

Tricolia pullus (da Costa) (Fig. 1*m*).

This species was referred to *Phasianella* by Jeffreys, who describes the "fry" as globular and distinctly umbilicate and states that they might be mistaken for a *Lacuna*. Specimens in a bowl at Plymouth laid eggs singly into the water like *Gibbula*. The egg is 0·14 mm. across.

Order MESOGASTROPODA

The eggs are contained in capsules or gelatinous masses occurring singly or in numbers. Very occasionally the animal is viviparous. The larva hatches as a veliger, as the veliger stage is passed within the egg covering and the young emerge in the crawling stage. In the free-swimming forms the velum is bilobed (Fig. 4*f*) or faintly four-lobed. Later it may be four-lobed or six-lobed (Fig. 4*g*, *h*). The veligers may remain for a long time in the plankton and the shell may have as many as eight whorls before metamorphosis. Some of the most important planktonic forms belong to this order.

Family LACUNIDAE

The species may be viviparous, or may hatch in the crawling stage or as veligers, remaining for a short or long time in the plankton. The velum is bilobed. The egg is surrounded by a membrane, an albuminous layer and an egg covering. There are usually several eggs in a gelatinous mass attached by the whole of one surface to a substratum; or, if planktonic capsules, one or a few eggs, the egg covering surrounded by a sheath.

Genus Lacuna

(Fig. 2*c*)

Jeffreys (III, p. 344) refers to *L. puteolus* (=*parva*) certain spawn and young which almost certainly belong to *L. vincta*, and again (p. 350), quoting Spence Bate, describes the young as hatching in the crawling stage—almost certainly *L. pallidula*. The spawn of the latter species has often been taken for that of *Littorina obtusata* which it resembles, although smaller and more delicate. Caullery & Pelseneer (1910) figured the spawn of *Lacuna pallidula* as that of *L. divaricata* (=*vincta*). Later, Pelseneer (1911) describes accurately the spawn of *L. pallidula* and its early embryology. These two species, *L. pallidula* and *L. vincta*, are apparently the only species whose spawn and development are known. The first hatches in the crawling stage, the second as a veliger with a fairly long planktonic life. The eggs are in gelatinous masses, several in each mass and scattered irregularly, the surface of the gelatinous mass hardening to a certain degree into a pellicle. The later crawling stage shows the two characteristic processes at the hind end of the foot. Hertling & Ankel (1927) and Hertling (1928) describe the spawn and newly hatched young of both *L. pallidula* and *L. vincta*. It is probable that at least one other British species of *Lacuna* has free-swimming veligers and spawn resembling that of *L. vincta*, since very similar egg masses of a different species have been observed at Plymouth between tide marks.

Lacuna vincta (Montagu)=*L. divaricata* Fab. (Figs. 2*c*; 4*e*).

The spawn of this species is well known and is usually regarded as typical of the genus. The adult is one of the commonest molluscs living between tide marks and below in shallow water, laying its familiar spawn rings on various weeds, brown, green and red. Meyer & Möbius (1872) describe the egg masses figuring them somewhat inadequately. Delsman (1914) gives a good description. All these workers quote *Zostera* as the substratum on which the eggs are laid. Hertling & Ankel (1927) found it chiefly on *Laminaria* and *Fucus serratus*. At Plymouth it occurs on all these and many others.

The newly laid spawn is in the form of a ring, very slightly spiral, covered with a thin lens-shaped pellicle (Fig. 2*c*). Sometimes this is somewhat oval in outline. The egg masses enlarge considerably as the larvae develop, reaching sometimes 9 mm. across. Hertling & Ankel give good figures. The number of eggs is significant—up to 1000–1200—while they are much fewer in *Lacuna pallidula*. Hertling has made important researches into the influence of various chemical and physical factors on the development of *Lacuna* and *Littorina* (chiefly *Lacuna vincta* (=*divaricata*)).

My own researches on *L. vincta* at Plymouth agree well with those of Hertling. The spawn is found from January to early summer and is usually of a creamy yellow colour (other egg masses which are pink or green almost certainly belong to another species). Spawn was laid in the Laboratory from

January to May and was always cream-coloured. Eggs laid on January 22 hatched on February 6 as free-swimming veligers with bilobed velum. The average size of the newly laid egg mass is 3 mm. across, increasing as development proceeds. The egg is surrounded by a membrane, an albuminous layer and an egg covering, and is about 0·18 mm. across. On hatching (Fig. 4*e*) the eyes, otocysts, foot, operculum and velum are all well formed and the mouth open. The shell has about one and a half whorls, clear, colourless and without sculpture. The velum is furnished with long cilia and has a brownish red border. The veligers grow quickly and remain for some time in the plankton, metamorphosing when the shell has about two and a half whorls. The shell of a young *L. vincta* which metamorphosed in the aquarium had three whorls, measured 2 mm. in height, was of a clear horn colour, and had the two long tentacles at the hind end well formed.

Lacuna pallidula (da Costa).

This species lays its eggs in thin gelatinous masses, oval or round, usually on *Fucus* and *Laminaria*, often with those of *Littorina littoralis* (=*obtusata*), which it closely resembles, although much smaller and with thinner walls. Good figures and descriptions are given by Hertling & Ankel (1927). The length of the spawn masses is 3·9–5·3 mm., and the breadth 3·3–4·5 mm. The number of eggs is 110–125 (Pelseneer), 60–140 (Hertling & Ankel). The newly laid eggs are 529–571 μ, gradually enlarging as development proceeds. The veliger stage is passed within the egg covering in the spawn mass, and the young emerge in the crawling stage. The species breeds in late winter, early spring and summer.

Genus Littorina

(Fig. 2*d*)

The species of this genus differ in outward appearance from *Lacuna* in the absence of posterior tentacles and of the umbilicus. The young crawling animal is easily identified by the absence of these tentacles. Jeffreys (III, p. 355) states that most of the species are oviparous and deposit their spawn on seaweeds, rocks or stones. As a matter of fact the only British species known to do this is *Littorina littoralis* (=*obtusata*). *L. saxatilis* (=*L. rudis*) is viviparous, *L. littorea* and *L. neritoides* have planktonic egg capsules from which hatch free-swimming veligers. Again in this genus we find as usual that the more the eggs are protected the fewer the number. *L. saxatilis* sends out a brood of about 37 young, *L. littoralis* with no free-swimming stage lays about 150 eggs, and *L. littorea* about 500. Linke (1933*a*) gives excellent descriptions of the eggs and their origin in all three species. Hertling & Ankel (1927) had previously supplied much information as to the egg masses of *L. littoralis*, whilst Delsman (1914) had worked out thoroughly the embryology of that species.

Littorina littorea (L.) (Fig. 2*d*).

The common periwinkle abounds on all our coasts. The errors of early workers in attributing the spawn of *L. littoralis* to this species are frequent and are carefully investigated by Hertling & Ankel (1927). Caullery & Pelseneer (1910) and Tattersall (1910) discovered the true nature of the spawn almost simultaneously and showed that *L. littorea* sends out planktonic spawn cases, each containing one to five eggs (very rarely, according to Linke, as many as nine). From these eggs free-swimming veligers hatch which remain in the plankton for some time and can be distinguished by certain characters. I have also observed this species laying egg capsules at Plymouth and both capsules and veligers are common in the coastal plankton. I have figured the eggs and larvae (Lebour, 1935*b*, figs. 7–9).

The capsule is shaped like a British infantryman's shrapnel helmet (Fig. 2*d*), and there may be 500 of these laid by one individual. It sinks slowly, those with one egg the slowest of all (Linke), and this is of distinct advantage to the mollusc in keeping in the surface layers for the purposes of distribution, and, when the eggs are hatched, for feeding. The capsule measures about 1 mm. across, or less, each individual egg measuring about 205μ. The egg develops into a veliger with a well-formed velum and spiral shell of about one and a half whorls, and at this stage the larva breaks through the coverings and hatches. Pelseneer (1911) gives a partial description of the early larva and the development of the egg. The shell is faintly striated spirally and is of a yellowish colour; the velum has long cilia round its border and is marked with a conspicuous and very characteristic dark purple patch on each lobe. The tentacles, eyes, otocysts, foot and operculum are all well formed. The larva remains for some time in the plankton, metamorphosing when it has about two whorls or rather more. Just before this it can either crawl or swim, and when crawling and the velum is withdrawn the purple pigment shows through the shell as two conspicuous hemispherical patches. Late larvae with brownish shells are common in the plankton near the coast, especially in spring. The species breeds at Plymouth from November to May, chiefly in February and March (Moore, 1937).

Subgenus *Littorivaga*

Littorina saxatilis (Olivi) (=*L. rudis*).

This species of many varieties has long been known to be viviparous, breeding throughout the year. It lives from well above high-water mark to extreme low water and has a wide distribution. The eggs are protected within the body of the parent in a brood sac at the lower end of the oviduct until the crawling stage and are few in number, 28 to 37 according to Linke (1935). Linke describes the genital apparatus and eggs. Delsman (1914) has also described the unsegmented eggs which resemble those of *L. littorea* and *L. littoralis* with a thin yolk, albuminous layer and the egg covering. Sometimes two or three embryos are in the same covering, rarely four. When ready to hatch the young break the covering with their radulae and emerge from the parent as small brown-shelled young with no velum.

Subgenus *Melarhaphe*

Littorina neritoides (L.).

The spawn of this species, which for some time was believed to be viviparous, has only lately been recognized. It is now known that it lays planktonic egg capsules, somewhat similar to those of *L. littorea* but much smaller and each containing only one egg. Dr Otto Linke (1935), of Leipzig, was the first to discover these capsules in specimens sent from Rovigno. Spawn and larvae are also described by Lebour (1935*b*, p. 373, figs. 1–5, 10, 11). It is very surprising to find planktonic egg capsules in a species with such a restricted range and usually living well above the high-tide level. At Plymouth, however, it is sometimes found in small rock cavities in water. The capsules are lens-shaped, rounded in the centre of each surface, more curved on one side than on the other, and 0·16 mm. across. Each capsule contains one egg covered with a membrane and floating in a nutritive fluid enclosed in a small circle, the rest of the capsule being outside it. The egg is 0·08 mm. across. The larva hatches as a veliger with a bilobed velum, and the shell has concentric striations with small dots in between.

Subgenus *Neritoides*

Littorina littoralis (L.) (=*L. obtusata*).

The spawn of this species is laid in kidney-shaped or oval masses on weeds, usually *Fucus serratus*, on which it lives in large quantities on all our coasts. Frequently the smaller spawn of *Lacuna pallidula* is seen near it. Delsman (1914) has described the embryology, and Hertling & Ankel (1927) and Linke (1935) have investigated the spawn in detail. It is one of the commonest egg masses but has often been taken for the spawn of other molluscs. Hertling & Ankel reproduce a very old drawing by Baster (1762) who was the first to describe and figure it. Tattersall (1910) and Pelseneer (1911) both knew it and the latter author figures it. The spawn, which has a slightly yellowish tinge, is transparent and is on an average 7 by 3 mm., enclosing about 90–150 eggs. The newly hatched egg is about 250μ, surrounded by a thin layer of yolk which apparently soon disappears. The young take three or four weeks to hatch, passing the veliger stage within the gelatinous covering and emerging in the crawling stage, biting their way out with the radula.

Family HYDROBIIDAE

(Fig. 2*e*)

The species of this genus either lay eggs in capsules similar to those of typical Rissoidae, or they are viviparous (in fresh water). Only the breeding of *Hydrobia ulvae* and *H. ventrosa* is known; the first has free-swimming veligers, while the second is viviparous.

Genus Hydrobia

Hydrobia ventrosa (Montague) (*H. Jenkinsi*).

This is a freshwater species, but is frequently found in streams near the sea. It is found with young in all stages inside it in a freshwater stream running down to the sea near Wembury, Plymouth. The species is included here as it is of interest in contrast with the common *H. ulvae* which has sessile egg capsules and a free-swimming veliger.

Subgenus *Peringia*

Hydrobia ulvae Perissant.

This species is very common in estuaries and brackish water districts. Meyer & Möbius (1872) were the first to record the egg capsules which were laid on neighbouring shells of the same species. Herdman (1888) also records it and Henking (1894) describes the eggs and young, his work being quoted by Simroth (1911). Specimens from the Plymouth estuaries have laid eggs in captivity, always on one another's shells. The egg capsule is lens-shaped and covered with sand grains, attached to the shell by its flattened base. Inside there may be three to seven eggs. The capsule is about 0·6 mm. across. The egg is covered by a thin membrane, and the eggs are together floating in an albuminous fluid within the capsule. The newly-hatched larva has a horny shell of about one and a half whorls, with tentacles, eyes, otocysts, foot and operculum, and is much like a young *Rissoa*. The velum is well developed and colourless. The late larva has not been described.

Family RISSOIDAE

(Fig. 2*f*)

All the members of this family whose breeding is known lay eggs in capsules, usually lens-shaped and attached by the flattened surface to a substratum. Occasionally they are oval or nearly spherical and attached only partially by one surface. Each capsule usually contains several eggs; the egg is enclosed in a thin membrane and all float together in an albuminous fluid surrounded by the fairly thick-walled capsule. The latter is thinnest in the centre of the free surface where the young break through on hatching. Occasionally the eggs are laid singly in a capsule, or two together, the capsule being oval or round. Where this occurs the young emerge in the crawling stage (*Cingula cingillus*, *C. semicostata*), but the larva usually hatches as a veliger with a bilobed velum. The veligers may remain for a short or a long time in the plankton, and typically attain two and a half whorls before metamorphosis, the velum always remaining bilobed.

The Rissoids, both on account of their immense numbers and because most of them stay in the plankton for some time, are of considerable importance. The very young herring feed largely on the newly hatched veliger of *Rissoa sarsii* (Lebour, 1934*a*), and huge numbers of old and young stages of many species are to be seen in the plankton at all times of the year—different species in different seasons. Most of the Rissoids inhabit the region between tide marks and the free-swimming young occur frequently in coastal or shallow-water plankton, but some are deeper water species and have a wide range. Some of the commonest coastal species occurring in the plankton are *R. parva*, almost the whole year round, *R. sarsii* in winter and spring, and, farther out, *Alvania punctura* in summer and autumn.

Lovén (1839) was the first to describe and figure the veliger of a Rissoid. This he ascribes to *Rissoa costata* (*Alvania crassa*), and it has the typical form of a late Rissoid larva, having about two and a half to three whorls and a moderate-sized bilobed velum. It might belong to any typical Rissoid species. This figure is reproduced by Simroth (1911). Fischer (1892) figures the spawn of *Rissoa membranacea*, and Pelseneer (1911) that of *R. parva*. Jeffreys (III, 1867) refers briefly to eggs and "fry" of several species, and I have myself described a number of eggs and larvae (Lebour, 1934*a*, 1936). *R. octona* (L.), not recorded for Britain, is shown by Meyer & Möbius (1872) to have typical spawn cases. They describe and figure it laid on *Zostera* and on the shells of its own species, and hatching as a free-swimming veliger.

Genus Cingula

Subgenus *Parvisetia*

Cingula fulgida (J. Adams).

The eggs and young are described and figured by Lebour (1936, p. 548, pl. i, fig. 7). The species is common in rock pools on algae between tide marks and the eggs are laid singly in small tough round capsules on corallines. The capsule is 0·32 mm. across and the egg 0·16 mm. across. As it develops the embryo enlarges considerably and the young hatches in the crawling stage. The newly hatched shell is dark brown with a yellowish operculum. The species breeds in April in the Laboratory.

Subgenus *Onoba*

Cingula semicostata (Montagu).

The eggs and larvae are described and figured by Lebour (1934*a*, p. 536, pl. iii, figs. 19–20). The species is common between tide marks, under stones and among hydroids and algae. Single eggs are laid in tough, oval, thick-walled capsules, usually fixed to small sand grains or mud particles. The capsule is 0·48–0·64 mm. long by 0·32–0·48 mm. broad. The egg in its membrane is 0·24 mm. across when newly laid. The veliger stage is passed within the capsule and the young emerge in the crawling stage. The shell of the newly hatched young is 0·30 mm. across, cream coloured and striated. The species breeds from March to May in the Laboratory and young in all stages are found throughout the year.

Cingula semistriata (Montagu).

The eggs and larvae are described and figured by Lebour (1934*a*, p. 536, pl. iii, figs. 15–18). The species is common between tide marks on hydroids and algae. The typical sessile lens-shaped capsules are 0·56–0·64 mm. across and 0·24 mm. high, and are colourless and transparent, containing from about 12–22 eggs, 0·08 mm. across when newly laid. The larva hatches as a veliger with a smooth unsculptured shell, about 0·10 mm. across. The animal and velum are colourless. Later veligers have two conspicuous lines below the suture on the body whorl of the shell and three processes at the back of the foot. Breeding in the Laboratory takes place in spring and autumn.

Cingula cingillus (Montagu).

The eggs and larvae are described and figured by Lebour (1936, p. 548, pl. i, figs. 8–10). They are abundant about high-water mark, sometimes above, on stony and pebbly ground. The eggs are in capsules laid in crevices of stones. The capsules are of typical shape but contain only two to four eggs. They are 0·64–0·72 mm. across, the egg being 0·16 mm. across. The young hatch in the crawling stage with brown shells with about two whorls, and the operculum yellow. The white variety is often found with the typical form; the spawn is similar, the young being colourless with a yellowish operculum. Breeding in the Laboratory takes place in spring.

Genus Alvania

All species whose young are known have sculptural apices. Certain adult Rissoids from Australia described by Powell (1930) and others mentioned by Thiele (1929) seem to be closely related to *Alvania* and have similar apices. Thiele places *A. cimicoides*, which is a British species, in the section *Acinulus*, subgenus *Alvania* in the genus *Rissoa*, and this species has a sculptured apex. *R. sarsii*, with its striated and dotted apex, should probably be placed here, although at present it is left in the genus *Rissoa* in accordance with Winckworth's classification. All known larvae of this genus remain long in the plankton.

Subgenus *Manzonia*

Alvania crassa (Kanmacher).

The eggs are not known, but the larvae have been described and figured by Lebour (1934*a*, p. 538, pl. iv, figs. 8–10; 1936, p. 549, pl. i, figs. 11, 12). It is fairly common in Plymouth Sound, usually below low-water mark. Larvae in all stages are common in the inshore plankton, usually in late summer and autumn. The newly hatched larva is 0·16 mm. across the shell, which has one and a half whorls and is sculptured with spiral lines with irregular divisions;

the animal and its velum are colourless. Later larvae have beyond the first whorl and a half interrupted striae on the following whorls near the periphery. They metamorphose after having attained about two and a half whorls, when the shell begins to have the adult sculpture.

Subgenus *Alvania*

Alvania cimicoides (Forbes).

The embryonic whorls are sculptured (Thiele, 1929).

Alvania jeffreysii (Waller).

The apex is blunt and marked with a vandyke pattern instead of having rows of punctures (as in *A. punctura*; see Jeffreys (IV, 1867, p. 15)).

Subgenus *Octona*

Alvania punctura (Montague) (= *Arsenia punctura*).

"The uppermost whorls exhibit under the microscope a few rows of punctures" (Jeffreys, IV, 1867, p. 17). The eggs and larvae are described and figured by Lebour (1934*a*, p. 537, pl. iv, figs. 1–7). The species is common at Plymouth below low-water mark and further out among bryozoa. The larvae are common in the plankton in summer and early autumn. The eggs have been seen laid on weeds in the Laboratory. The capsules are of typical form, small and thick-walled, 0·32–0·48 mm. across, rather high, containing about 12–14 eggs, 0·06 mm. across. The newly hatched larva has a shell of about one and a half whorls, sculptured with spiral striae and dots in between, similar to that of *Rissoa sarsii*, but smaller. Beyond the first whorl and a half there are small raised spots on the whorls, by which it can be distinguished at once from *R. sarsii*. The animal is yellowish white, and the velum colourless, the shell becoming dark horn colour.

The larval shell when metamorphosis is about to take place is 0·64 mm. long. The larvae remain for a long time in the plankton.

Genus Rissoa

(Fig. 2*f*)

All known species have smooth apices and free-swimming larvae except *R. sarsii*, which has a sculptured apex and should almost certainly be placed in the genus *Alvania*.

Subgenus *Turboella*

Rissoa albella Lovén.

"The spawn cases are generally solitary, semi-globular, membranous and light yellowish brown; the fry emerge from a large hole in the top which appears when they are developed" (Jeffrey, IV, 1867, p. 29).

Rissoa sarsii Lovén.

The eggs and larvae are described and figured by Lebour (1934*a*, p. 533, pl. i, figs. 1, 9–21 (not figs. 2–8); 1936, p. 550, pl. i, fig. 13). The adults are not often seen, but they occur between tide marks. The larva is one of the commonest in the winter and spring coastal plankton, forming to a large extent the food of the larval herring in winter. The eggs are in typical lens-shaped capsules 0·48 mm. across, each containing 10–14 eggs, 0·09 mm. across. The newly hatched larva has a shell 0·12 mm. across, with spiral striae and dots in between. Beyond the first whorl and a half the upper part of the shell is smooth, the periphery and just below having rows of interrupted striae. The shell is colourless and transparent, becoming pale horn colour with a dark brown mouth. The velum is at first colourless, becoming bordered with a fine dark band, occasionally absent on one side. The animal is yellowish with dark brownish purple pigment at the base of the foot in the older larvae which possess the mantle tentacle and a very long posterior tentacle. Metamorphosis takes place when the shell is 0·48 mm. with two and a half to three whorls.

Rissoa inconspicua Alder.

The egg capsules are described and figured by Meyer & Möbius (1872) and the free-swimming larvae described. The eggs and larvae are described and figured by Lebour (1934*a*, p. 533, pl. iv, figs. 13–15). The species is common in shallow water below low-water mark and beyond. The egg capsules are of typical form, 0·48–0·64 mm. across and were laid in the Laboratory on *Zostera*. There were about six to nine eggs in each capsule. The capsules were laid either on the shell of another individual, or on pieces of debris. The eggs were 0·08 mm. across. The newly hatched larva has a smooth unsculptured shell. The velum is colourless at first, but later bordered with brown. Older larvae have two faint spiral lines round the periphery of the shell. The larvae are common in the plankton, especially in early autumn. The adults breed in captivity in October. Newly metamorphosed animals have the purple apex to the shell characteristic of the adult.

Rissoa parva (da Costa).

"The spawn capsules are semicircular, yellowish brown and sometimes deposited on the shells of other individuals" (Jeffreys, IV, 1867, p. 23). Caullery & Pelseneer (1910) and Pelseneer (1911), describe the spawn. The eggs and larvae are described and figured by Lebour (1934*a*, p. 532, pl. iii, figs. 1–7). The capsules are 0·64 mm. across or slightly larger, containing 6–50 eggs, 0·09 mm. across. The spawn is usually laid on weeds, both brown and green, in almost any month of the year. The newly hatched larvae have smooth unsculptured shells with one and a half whorls. The velum is colourless; there is a fine line round the periphery of the late larval shell, and dark purple at the base of the foot. The larvae metamorphose when the shell is 0·48 mm. long, with nearly four whorls. This is the commonest of all the Rissoids, occurring between tide marks down to extreme low water and sometimes slightly beyond.

Rissoa guerini Récluz.

The eggs and larvae are described by Lebour (1934*a*, p. 532, pl. iii, figs. 8–14). The species is fairly common among weeds between tide marks. The eggs were laid on weeds in the Laboratory from February to April. The capsules are of typical form, 0·96–1·4 mm. across, containing 80–100 eggs, 0·09 mm. across. The newly hatched larva has a colourless, smooth and unsculptured shell 0·16 mm. across. The animal is colourless at first, but in a few days the velum becomes spotted with dark brown. The larva metamorphoses when the shell has about three and a half whorls, the foot having a dark patch at the base. The larvae are common in the plankton from spring to autumn.

Subgenus *Rissoa*

Rissoa membranacea (J. Adams).

Fischer (1892) briefly describes and figures the egg capsules which are of typical form. The eggs and larvae are described and figured by Lebour (1934*a*, p. 529, pl. ii, figs. 6–15). This species formerly occurred commonly on *Zostera* at Plymouth, but it has not been seen for the last few years on account of the disappearance of *Zostera* from disease. It probably breeds throughout the year. The capsules are 1·4–1·6 mm. across and contain 40–60 eggs, 0·13 mm. across. The newly hatched young have shells 0·32 mm. across, the animal and velum being colourless. The larva remains only a very short time in the free-swimming stage, metamorphosing when the shell is about 0·37 mm. across and has only two whorls.

Genus Barleeia

Barleeia unifasciata (Montagu) (=*Barleeia rubra*).

The eggs and larvae are described and figured by Lebour (1934*a*, p. 537, pl. iv, figs. 11, 12). The species is common on weeds at extreme low tide, locally, usually with *Rissoa parva*. The egg capsules are round, 0·56 mm. across, and attached to weeds, *Fucus* and *Calliblepharis*. There is only one egg, 0·32 mm. across, in each capsule. The larva is hatched in the crawling stage. Adults spawned in the Laboratory in March and April. The newly hatched shell is dark brown with a reddish-brown operculum and one and a half whorls; it is 0·42–0·48 mm. across.

Family TORNIDAE

Genus Tornus

Tornus subcarinatus (Montagu).

The eggs are unknown. The larvae are described by Lebour (1936, p. 552, pl. i, figs. 14–16). They are common in the inshore plankton. The veliger remains in the plankton until the shell has about three whorls, the first two being smooth and the third marked with conspicuous raised striae. The shell is 0·48 mm. across when the animal is ready to metamorphose. The velum is bilobed, fairly large, and colourless; the animal is very dark. The late larva shows the typical bilobed pallial tentacle.

Family SKENEOPSIDAE

Genus Skeneopsis

Skeneopsis planorbis (Fabricius) (Fig. 2*g*).

Pelseneer (1926) states that the young hatches in the crawling stage. Linke (1933*b*) describes and figures the spawn and the young which confirms Pelseneer's statement. The egg capsules and young have also been obtained in the Plymouth Laboratory. The capsules are round, 0·48 mm. across, and attached to weeds. The young when ready to hatch have brown shells 0·32 mm. across. The species breeds throughout the year. It is very common in rock pools, high up between tide marks.

Family OMALOGYRIDAE

Genus Omalogyra

Omalogyra atomus (Philippi) (Fig. 2*b*).

Jeffreys (IV, 1867, p. 71) states that he found dried up spawn capsules inside the upper cavity of the last whorl, "much larger than the capsules that I have seen in my *Rissoa*". The species is common in pools high up between tide marks, often with *Skeneopsis planorbis*. Capsules have been seen in the same position as that described by Jeffreys, but they were much smaller. It is probable that these were the egg capsules, but they have not been hatched out. The young probably hatch in the crawling stage, for very young crawling young with shells only 0·16 mm. across have been seen; it is almost certain that there are no free-swimming stages. The young are found throughout the year.

Family RISSOELLIDAE

Genus Rissoella

Rissoella diaphana (Alder).

Jeffreys (IV, 1867, p. 60) states that "the spawn deposited by one individual consisted of only two ova, which are enclosed in a hemispherical case". The eggs and young are described and figured by Lebour (1936, p. 552, pl. i, fig. 17). The species is common in the rock pools high up between tide marks. The eggs were laid in the Laboratory in spring and summer. The capsules are hemispherical, thick, colourless, 0·48 mm. long and about 0·25 mm. broad;

they are attached by a flat base to weed (green or red). Each capsule contains two eggs, about 0·2 mm. across, with egg membrane and albuminous layer, enclosed in an egg covering. The young emerges in the crawling stage, with a shell 0·24 mm. across, of a pale horn colour. The newly hatched animal has two pairs of tentacles and a conspicuous black patch dorsally on the left side. The young in all stages are to be found with the adults in numbers in spring and summer.

Subgenus *Jeffreysina*

Rissoella opalina (Jeffreys).

Jeffreys (IV, 1867, p. 61) states that "the spawn deposited on leaves of *Laminaria* is semi-oval in shape with a large hole in the middle. When ripe it forms a thick mass, and contains an immense number of yellowish unispiral shells which are agglutinated together by a gelatinous matrix."

Family TURRITELLIDAE

Genus Turritella

Turritella communis Risso (Fig. 2*h*).

The eggs and larvae are described and figured by Lebour (1933*d*, p. 499, pl. i, figs. 1–8). The species is common on muddy ground. Eggs have been laid and hatched in the Laboratory; they are also sometimes found in tow-nettings having been carried up from the bottom mud. The spawn is in grape-like clusters of round gelatinous capsules held together by threads, each capsule being 0·64–1·12 mm. across, and pale pinkish brown from the pinkish eggs which show through. There are 6–20 eggs or more, 0·10 mm. across, in each capsule; some hundreds of capsules are laid by one individual. The egg has a membrane and floats freely in an albuminous fluid. The newly hatched larval shell has one whorl, smooth and colourless; the animal and the bilobed velum are colourless. It stays only a short time in the plankton. The crawling young have a shell of two and a half whorls and a very broad apex, the last whorl beginning to be ribbed spirally, the ribs being pitted in lines. The spawn is common round Plymouth in summer.

Family CAECIDAE

Genus Caecum

Caecum imperforatum (Kanmacher).

Jeffreys (IV, 1867, p. 78) states that "the spire of the fry has two whorls—the inner being sometimes broken off so as to make the centre pervious". The embryonic whorls are cast off in the older individuals, the adult having no spire and the aperture being closed with a shelly flat plate. The eggs are not known. The larva is described by Lebour (1936, p. 553, pl. ii, figs. 1–5); it is common in the inshore plankton. The veliger has a bilobed velum with a purple border; the shell is a flat spiral and the animal has a yellow digestive gland and is dark purple near the head. It is ready to metamorphose when there are two and a half whorls, and the shell is 0·32 mm. across. Specimens 1·0 mm. in length were found at Plymouth with a coiled spire still present.

Family CERITHIIDAE

Genus Bittium

Bittium reticulatum (da Costa).

Meyer & Möbius (1872) have described and figured the spawn as a flat slimy spiral coil, *ca.* 3 mm. across. Lo Bianco (1888) describes it as a white ribbon irregularly folded on itself and states that they breed from January to May. Free-swimming larvae almost certainly belonging to this species occur commonly in the plankton in spring and summer, usually in shallow water (Lebour, 1936, p. 553, pl. ii, fig. 6). The late larva has a pale horn-coloured shell of two and a half whorls, the outer lip being produced as a process as in *Cerithiopsis* and *Triphora* though not so pronounced (see below, pp. 137–138). The velum is colourless and bilobed. The larva metamorphoses when the shell is 0·32 mm. long.

Family CERITHIOPSIDAE

All the three members of this family known from Plymouth live among sponges, and two of them (the eggs of the third being unknown) lay their eggs in the sponge. The larvae remain for a long time in the plankton, attaining several whorls before metamorphosing. The larval shell is sculptured or smooth, with a shovel-shaped projection of the outer lip to support the velum which is bilobed.

Cerithiopsis tubercularis (Montagu) (Fig. 2*j*).

The larvae are described and figured by Lebour (1933*c*, p. 496, pl. i, figs. 8–11) and later the eggs also (Lebour, 1936, p. 544, pl. v, figs. 9–10). The species is common, living among sponges, chiefly *Hymeniacidon*, on which it lays its eggs. Holes are made in the sponge and egg capsules, 0·5–1 mm. across, laid in them. The capsules are full of minute opaque white eggs, 0·06 mm. across. The larvae are common in the plankton, both inshore and offshore; attaining four to four and a half whorls before metamorphosis. The shell is smooth and pale horn colour. The last larval whorl has a large outgrowth from the outer lip bent over the shell mouth; this is marked with concentric striae dotted in between, and replaced at metamorphosis with the reticulated sculpture of the adult. The late larva is 0·64 mm. long. There is a dark line at the suture of the larval whorls and on the columella, and the aperture is dark brown. The animal is pale yellowish and the velum colourless, with round and unequal lobes; the foot is mottled with grey on the sole. Breeding takes place in spring and summer.

Cerithiopsis barleei Jeffreys.

The eggs and larvae are described and figured by Lebour (1933*c*, p. 497, pl. i, figs. 12, 13, pl. ii). The species is common in shallow water on the sponge *Ficulina ficus*, in which it lays its eggs. The egg capsules are laid in holes in the sponge; they are 1·5 mm. across, and placed at intervals of about 5 mm. or more apart. There are about 200 eggs in each capsule. The newly hatched larval shell is 0·14 mm. across with about one and a quarter whorls; it is light brown, and its surface is covered with raised dots, except at the base, where it is striated. The outer lip is slightly drawn out at first, but later a large shovel-shaped process is formed. The velum is colourless with unequal round lobes. The animal is pale yellowish. The third whorl of the shell is ribbed. Late larvae with four and a half whorls are ready to metamorphose. The newly metamorphosed shell is 0·64 mm. long. The larva remains a long time in the plankton. Breeding takes place during spring, summer and autumn.

Cerithiopsis jeffreysi Watson.

This species occurs among sponges at Plymouth, but its eggs and larvae are unknown. Watson (1885) figures the apex of the adult (corresponding with the larval shell) as smooth and having several whorls.

Family TRIPHORIDAE

Genus Triphora

The only species of this genus whose eggs are known is *Triphora perversa*; they were found by Pelseneer (1926). Many pelagic larvae have been recognized. All appear to remain long in the plankton, having many whorls before metamorphosing. Several larval shells of this genus have been ascribed to *Sinusigera* which is only a larval genus. Vayssière (1930) recently figured *Sinusigera dautzenbergi*, Craven (1877) *Sinusigera perversa* (later 1884, referred to *Triphoris* = *Triphora*) and Boas (1886) *Limacina turritelloides*; all belong to *Triphora*. The embryonic whorls are elaborately sculptured.

Triphora perversa (L.).

Pelseneer (1926) described the eggs, laid in a layer on a dead shell of *Pectunculus*, and figured the newly hatched larvae which were veligers having a sinistral shell and animal. Fischer (1884) states that the larva remains in the plankton until it has eight or nine whorls. The larvae are described by Lebour (1933*c*, p. 291, pl. i, figs. 1–7); they are common in the Plymouth plankton both inshore and offshore. Breeding takes place in spring, summer and autumn. The early larva is 0·16 mm. across with a brown sinistral shell covered with raised dots, except at the base, where there are spiral striae; the outer lip is produced into a conspicuous process. The animal is pale yellowish white, later having grey on the foot. The velum is colourless with round lobes, becoming unequal. The larva with two whorls has a shell 0·2 mm. long, that with six whorls is 0·64 mm. long. Beyond the first whorl and a half the shell is sculptured with longitudinal striae and keeled, the last whorl before metamorphosis takes place being tuberculated as in the adult. They remain for a long time in the plankton.

Family EPITONIIDAE

Genus Clathrus

Clathrus clathrus (L.) (Figs. 3*d*, *e*).

The spawn and newly hatched larvae are described and figured by Vestergaard (1935, p. 221, figs. 6, 7) who got the adults to lay in an aquarium with sand at the bottom and the young to hatch. The spawn described by her, 3 cm. long, is in a long winding string of triangular capsules, covered with sand grains and containing many eggs. The egg capsules are 2 mm. high. The newly hatched larvae have bilobed vela and smooth shells of about one and a half whorls. The shell of the newly hatched young is 0·15 mm. across. On June 10 1937 some spawn was collected at the Salstone, in the Salcombe Estuary. The parent was found underneath attached by a slimy thread to the egg capsule. Several other similar strings were also found, all lying on mud near green weed. The capsules differed considerably from those described by Vestergaard, for they were covered with fine mud instead of sand and were polygonal and very irregular, only occasionally being triangular. Each mass of spawn covered a space of about 2–2½ in. The capsules were from 2 to 4 mm. across at the widest part and strung on a gelatinous thread like a necklace (Figs. 3*d*, *e*). It is probable that mud is the natural habitat for this species, and that Vestergaard's aquarium, provided with sand, was unnatural. Her figure shows much more regular triangular capsules than the Salcombe specimens. The eggs, 0·48 mm. across, hatched out on June 24, the veligers corresponding with those described by Vestergaard. Eggs were also obtained in August.

Family IANTHINIDAE

Genus Ianthina

Ianthina britannica Forbes & Hanley.

This species only rarely occurs off our coasts, mainly on the west and south, but usually only empty shells are seen. The animal secretes from the foot a foamy apparatus formed of air cells which serves as a float. In the female this is used as a raft for the enormous number of eggs which are enclosed in capsules and attached to the under surface from which they hang down

(Jeffreys, IV, p. 174). Many authors have written about the eggs and raft, some of the most recent being Pelseneer (1911) and Simroth (1911). It is figured by Fischer (1887, p. 92) and others.

Family EULIMIDAE

The larvae belonging to this family remain for some time in the plankton, have smooth shells and a velum with two rounded lobes. The first larva recognized as belonging to *Eulima* was taken in Norway by Lovén (1844), who identified it as *E. distorta* (=*Balcis devians*). It is not certain, however, that this is the right species, as it does not agree with those from Plymouth. Unidentified larvae belonging to the genus *Balcis* are sometimes found at Plymouth as veligers, besides those described below.

Genus Balcis

Balcis alba (da Costa) (=*Eulima alba*) (Fig. 2*k*).

The eggs and larvae are described by Lebour (1935*a*, p. 65, pl. i, figs. 1–10). The adult is commonly dredged off Plymouth. The eggs have been laid in the Laboratory in very thick-walled, oval capsules, 3 by 2·5 mm., colourless and opaque, containing hundreds of pinkish eggs, 0·10 mm. across, enclosed in a membrane and floating in an albuminous fluid. The newly hatched larva has a shell 0·16–0·18 mm. across, with one and a half whorls; it is smooth, colourless and transparent. The apex is very broad. The animal has two conspicuous dark streaks above the mouth; the digestive organs are dark, and the velum bilobed and colourless. The shell has five whorls before metamorphosing and is 0·66–0·72 mm. long. The larva remains a long time in the plankton. It is common inshore and offshore in spring and summer at Plymouth.

Balcis devians (Monterosato) (=*Eulima philippi*).

The larvae are described and figured by Lebour (1935*a*, p. 68, pl. i, figs. 11–15). They are common in the inshore plankton in spring and summer at Plymouth. They much resemble *B. alba* but have a blunter spine and no black pigment in the animal. The digestive organs are pale yellow. Metamorphosis takes place when there are about four whorls.

Family STYLIFERIDAE

Genus Pelseneeria

(Fig. 2*l*)

Most of the species known live on the tests of echinoderms and lay their eggs in gelatinous masses between the spines (Lamy, 1928, p. 180).

Subgenus *Rosenia*

Pelseneeria stylifera (Turton) (Fig. 2*l*).

Jeffreys (IV, p. 194) describes the egg masses. The eggs and larvae are described and figured by Lebour (1932*b* as *Stilifer stylifer*, p. 117, pl. i, figs. 1–7). The Plymouth specimens were living on *Psammechinus miliaris*. The eggs are contained in triangular cushion-shaped capsules, colourless and transparent, about 1·2 by 1·1 mm., with a stalk for attachment. Each capsule contains from 60 to 80 eggs, 0·1 mm. across; they are colourless, with egg membrane, all floating in a fluid in the capsule. The young hatched in the Laboratory had brownish transparent shells of one and a half whorls, about 0·13 mm. across. The velum is bilobed and colourless. The animal is colourless. The shape of the shell closely resembles the newly hatched shell of *Balcis alba*, with a wide apex.

Family PYRAMIDELLIDAE

All the members of this family have reversed apices, the planktonic young in their early stages having a sinistral shell and a dextral animal, the shell later also becoming dextral. The early young are thus easy to recognize, at any rate in British waters, where the only truly sinistral planktonic larva is that of *Triphora perversa*. All the known larvae of the Pyramidellidae are planktonic, the shell being colourless, transparent and smooth. Several have been found at Plymouth, but most of them are not identified as species. Pelseneer (1911) has described irregular masses of eggs in the foreign parasitic species *Angustispira spengeli* on *Meleagrina* and *Odostomia tellinae* on *Tellina*. The British species whose spawning is known lay irregular egg masses or lenticular capsules. The egg, with a thin membrane, is enclosed in an egg covering with a very thick layer of albuminous fluid between; it floats in a fluid within the capsule.

Genus Chrysallida

Subgenus *Parthenina*

Chrysallida decussata (Montagu) (= *Pyrgulina decussata*).

The eggs and larvae are described by Lebour (1936, p. 556, pl. ii, figs. 11–15). The adult is fairly commonly dredged from the outer grounds near Plymouth. Eggs laid in the Laboratory were in lens-shaped capsules, colourless and transparent, 0·24–0·35 mm. across, and attached by the lower surface to the glass. Each capsule had from four to eight eggs, about 0·09 mm. across. The young when nearly ready to hatch had colourless shells with about one and a half whorls. The animal is colourless, the velum bilobed. It is sometimes found in the plankton after metamorphosis with two to two and a half whorls, beginning to be sculptured and becoming dextral.

Genus Odostomia

Subgenus *Brachystomia*

Odostomia eulimoides Hanley.

The eggs and young are described by Lebour (1932*b*, p. 118, pl. i, figs. 9–16). The eggs are common on *Chlamys opercularis* and, more rarely, on *Pecten maximus*, being laid in irregular gelatinous masses about 1 mm. across on the ears and valves. These masses are clear and colourless, each containing many colourless eggs, 0·16 mm. across the covering. The newly hatched larvae have transparent colourless shells of one and a half whorls and are 0·16 mm. across. The animal is colourless, and the velum bilobed. It has three and a half whorls before becoming dextral and metamorphosing.

Genus Turbonilla

Turbonilla elegantissima (Montagu) (*Turbonilla lactea*).

The crawling young are described and figured by Lebour (1936, pl. ii, figs. 16–17). They are 0·25 mm. across and the shell is already dextral; therefore the free-swimming stage, which is probably present, must be very short. The adults are commonly dredged in shallow water in muddy ground with stones.

Subgenus *Tragula*

Turbonilla fenestrata (Jeffreys).

Jeffreys (IV, p. 158) describes the egg capsule as "semiglobular, attached by its round and broad base, membranous and thin. When the fry are developed, they find their way out through an oval hole in the centre of the upper part, which then becomes enlarged from what was at first a narrow slit."

Several different planktonic larvae belonging to the Pyramidellidae are found at Plymouth; they are described and figured by Lebour (1936, p. 557, pl. ii, figs. 18–22). All have a bilobed velum, two to two and a half whorls, and a sinistral shell.

Family TRICHOTROPIDAE

Trichotropis borealis Brod. & Sowerb. The breeding of this species is unknown in Britain. Thorson (1935, pp. 50–2, figs. 52, 54) has described and figured the eggs and larvae from East Greenland. The capsules are in clusters of two to four; round and oval in shape, with an irregular exit hole; they are deposited on empty bivalve shells. In all seen the hole was open and probably some larvae had escaped. From two to thirteen embryos were seen in each capsule. The young hatch in the crawling stage and have peculiar conchiolin membranes running in spirals on the whorls which are worn off in most of the adults. Thorson (pp. 52–4) also describes somewhat similar capsules and larvae in *T. conica*, attached to sabellid tubes.

Family CAPULIDAE

Genus Capulus

Capulus ungaricus (L.) (Fig. 4*d*).

Jeffreys (III, p. 271) states that the eggs are in little capsules under the body of the parent, fixed by a membrane in front of the foot. Lo Bianco (1888, p. 416) gives a similar description. Odhner (1914) describes the eggs and newly hatched young and figures the latter which has a well-developed bilobed velum.

On May 5 1937 a small specimen of *Capulus ungaricus*, 4 mm. across, was taken on a shell of *Arca* (*Barbatia*) *lactea*, dredged on Stoke Point Grounds in red stone. Although so small it was guarding its eggs under the shell in front of the foot. The egg mass measured 2·5 mm. across and was full of developing eggs, each egg being about 0·2 mm. across. These hatched on June 11, and it was surprising to find that the larvae were provided with an echinospira shell (a description of the echinospira larva will be found on p. 147). As this type of larva with an accessory shell has only been known hitherto in the Lamellariidae and Triviinae it upsets one's ideas considerably for either *Capulus* has been wrongly classified and should be placed near the Lamellariidae, or we must expect to find echinospira larvae in other groups. Odhner makes no mention of the echinospira and figures the larva without one. As it is very thin and transparent it may have been overlooked.

When newly hatched the echinospira shell is 0·4 mm. across, the true shell inside it being 0·24 mm. The echinospira (Fig. 4*d*) is transparent, gelatinous, and almost spherical, much like that of *Velutina* described below. The surface is covered with minute round spots which appear to be perforations for some secretion, as droplets stand out as though raised up on small hairs. The spots are arranged irregularly but are inclined to be radial. The developing alimentary canal is very dark, the velum colourless and well developed, and slightly indented in the centre of each lobe which projects beyond the echinospira. The larva is a powerful swimmer and lived in a bowl with small flagellates which it ate freely, the stomach and intestine being well developed. Although they lived for more than a fortnight they did not grow perceptibly and soon died.

The presence of the echinospira in *Capulus* is most interesting and may entail its being placed in the Lamellarioidea of Schindler (see p. 147). Its larva is quite unlike that of *Crepidula* or *Calyptraea*, in both of which genera the adults guard their eggs in the same way. *Crepidula fornicata* has a free-swimming veliger but no echinospira, according to the description; *Calyptraea* hatches in the crawling stage.

Family CALYPTRAEIDAE (L.)

The eggs are described by Audouin & Milne-Edwards (1832), Lo Bianco (1888) and Fischer (1892), the last worker figuring them. The eggs and larvae are described by Lebour (1936, p. 554, pl. ii, figs. 24, 25). The capsules are triangular, very soft-walled, fixed in a bunch by their narrow ends to a substratum, usually a stone, and covered by the parent with the part of the body in front of the foot. The capsule is transparent and colourless, 3–3·5 mm. long, pointed at the fixed end and broad at the free end. Each contains about 12–25 eggs, 0·48 mm. across, with a thin membrane, and floating in the fluid contained by the capsule. The veliger stage is passed within the capsule, the young emerging in the crawling stage. The shell has rather more than one whorl, about 0·64 mm. across; it is whitish, and the animal is colourless or yellowish white.

Lamy (1928) mentions other foreign species of *Calyptraea* having similar eggs.

Genus Crepidula

Crepidula fornicata (L.) (Fig. 2*m*).

The eggs and larvae are described by Conklin (1891, 1897), who worked at its embryology. The eggs are contained in somewhat balloon-shaped capsules 3·5 mm. across, united in a branch by their stalks on a common stem fastened to a stone or shell and covered by the parent. They are figured by Ankel (1935*a*). The capsules are thin and delicate, and cream in colour; each has about 250 eggs, *ca.* 0·16 mm. across. About 72 capsules are laid by one individual. The eggs have a thin membrane, and float in a fluid within the capsule. The larva hatches as a veliger and remains some time in the plankton; it is figured by Orton (1912–13). The larval shell is spiral; the velum is large and bilobed; there are regular pigment spots on the larva, green, red, brown, or black (Conklin).

Family APORRHAIIDAE

Genus Aporrhais

Aporrhais pespelicani (L.) (Fig. 4*h*).

Jeffreys (IV, p. 250) describes the young shell. The eggs and larvae are described by Lebour (1933*d*, p. 503, pl. ii, figs. 1–10). The species is common on mud near Plymouth. It breeds in March and through spring and early summer. The eggs were laid in captivity, but the larvae from them probably hatched prematurely as they had no shell and the velum was almost round. The late larvae are common in the plankton. The eggs, 0·24 mm. across, are laid singly, or two or three together, attached to sand grains or small pieces of debris; they have a thin membrane, an albuminous layer and a tough outer covering, and are transparent and yellowish. The larvae from the plankton have a four-lobed velum, with long lobes, each with a large brown spot at the corner; the shell is smooth, 0·56 mm. across, with a broad apex. The late larva has a six-lobed velum, each lobe having a large dark spot at the end and a dark brown border. The shell, about 1·4 mm. across, has the last whorl beginning to be spirally striated. It can either crawl or swim. At 1·5 mm. it metamorphoses, and the animal can be recognized as an *Aporrhais*. It has long tentacles, and a conspicuous proboscis, beginning to be red; the foot is pointed behind, the shell spirally striated. The larva remains long in the plankton.

Family NATICIDAE

(Fig. 3*c*)

All the species whose breeding is known lay their eggs in sandy spirals in which the eggs are glued, usually several in a capsule. The eggs in all known species are covered by a thin membrane, albuminous layer and egg covering, all floating in a fluid within the capsule. These sandy spirals were a great puzzle to the old naturalists but their true nature has been known for some time. Jeffreys (IV, p. 212) describes the spawn. Pelseneer (1906) describes and figures larvae from the Bay of Biscay which he attributes to this genus; they are figured and referred to by Simroth (1911) in his Gastropoda in *Nordisches Plankton*. Thorson describes the eggs and larvae of three species from East Greenland, all of which have sandy egg spirals but hatch in the crawling stage. These include *Natica groenlandica* which is also a British species but whose spawn and larvae were not known. Odhner (1914) describes the spawn and figures the newly hatched veliger of *N. maculata* (or *millipunctata*). This is not British but closely related to our British species. When still in the egg the larva has a four-lobed velum with long lobes; the foot is strongly developed, and the animal is able both to swim and crawl when taken out of the capsule. In the plankton it is 1·4 mm. across the velum, the shell being 0·8 mm. Of the two veligers found at Plymouth, one has been attributed to *N. catena*, the other to *N. poliana*, the two common species. The identification is not certain as they have neither been reared from the egg nor brought through to metamorphosis.

Genus Natica

Subgenus *Lunatia*

Natica catena (da Costa).

The spawn of this species is well known and often found at Plymouth in sandy bays where the adults are common below low-water mark. Jeffreys (IV, p. 213) describes the spawn and "fry". Ankel (1930) has described the spawn, developing egg and young; some of the eggs in the capsules devour the others (nurse eggs) so that only a few hatch out. Breeding takes place in spring and early summer. The egg coil forms a more or less complete spiral, about 130 to 160 mm. long and 30–40 mm. broad, being 70–80 mm. across the spiral. Eggs in the coil are contained in capsules, 2 mm. across, placed regularly one against the other and finally containing 12 to 15 young *Natica* which hatch out at intervals of 2 or 3 days (Ankel). The eggs are 0·16 mm. across in the egg covering. Hertling (1932) gives a good photograph of the spawn, and Ankel (1930) figures the young larva from the egg which is hatched as a veliger with a bilobed velum.

The planktonic larva, attributed to this species, is described and figured by Lebour (1936, p. 558, pl. ii, figs. 26, 27). It is common in the inshore plankton in spring; late stages about to metamorphose are sometimes found in summer. The veligers are rather like those of *Nassarius reticulatus* (see below) but are always distinguishable by the absence of a shell siphon (canal), and in the younger stages there is only a very small projection on the outer lip, so conspicuous in *Nassarius*. The velum is bilobed, not very large, with a thick purple-brown border. The late larvae are 0·48 mm. across the shell with two and a half whorls. Soon after this stage it can both crawl and swim and then metamorphoses.

Natica pallida Brod. and Sowerb. (=*N. groenlandica* Möller).

Thorson (1935, p. 55) has described the eggs and larvae from East Greenland; the spawn forms flat semicircular sandy masses about 55 mm. wide and 12–13 mm. broad. As most of those found were imperfect the spawn may form more than one complete ring. 12–28 capsules were found in a mass, each capsule containing one egg, about 2·25 mm., with a large amount of nutritive fluid and no more eggs. They are deposited freely on the sea bottom. The young emerges in the crawling stage; it has a large umbilicus and radial sculpture (Thorson, figs. 60–1).

Natica poliana Chiaje (Fig. 3*c*).

(*Natica alderi* of Forbes & Hanley and *Natica pulchella* of Hertling.)

The species is common at Plymouth both inshore and offshore. Hertling (1932) has described the eggs and newly hatched larvae. There are no nurse eggs. The spawn is frequently found in sand round Plymouth. It is very much flattened, usually forming an incomplete slightly spiral sandy ring, about 25 mm. across and 7·8 mm. wide. The eggs are 0·24 mm. across the covering. The newly hatched larva is described by Hertling; it has a bilobed velum, apparently colourless. Late larvae, which are common in the plankton, are ascribed to this species and figured by Lebour (1936, p. 559, pl. ii, figs. 28, 29); they are 0·8–1 mm. across shell. At about 1 mm. there are three and a half whorls and the larva can swim or crawl and is ready to metamorphose. The velum is at first small and only slightly four-lobed, but it grows out into four very long lobes, each with a dark brown spot at the end. The late larva is very like that of *Nassarius incrassata*, differing in the same way as is shown for *Natica catena*. It is a very important member of the plankton.

Family LAMELLARIIDAE

(Figs. 4*a–d*)

Following Winckworth (1932) the families Lamellariidae and Cypraeidae have been retained, but the latest classification by Schindler (1936) which is very important and significant places the genera *Erato*, *Trivia*, *Lamellaria* and *Velutina* as follows:

Stirps CYPRAEACEA; Superfamily LAMELLARIOIDEA

Eratoidae { Eratoinae: Eratoini:—*Erato*.
Triviinae: Triviini:—*Trivia*.

Lamellariidae { Lamellariinae:—*Lamellaria*.
Velutininae:—*Velutina*.

He places the true species of *Cypraea* in the superfamily Cypraeoidea, including *Simnia*. This, with other anatomical characters, takes into account the echinospira larva present in *Lamellaria*, *Velutina*, *Erato* and *Trivia*, but not in the true species of *Cypraea*. Hitherto, only members of the superfamily Lamellarioidea, as given above, were known to have echinospira larvae, but as is shown above (p. 143) in June 1937 it was found that the larvae of *Capulus ungaricus*, hatched in the Plymouth Laboratory, also possessed an echinospira shell, very similar to that described in *Velutina*. This interesting discovery may result in the systematic position of *Capulus* being revised and its being placed in the Lamellarioidea near *Velutina*, or it may be that other echinospira in other families are still to be discovered.

The essential feature of the echinospira larva is the presence of an accessory larval shell, the so-called echinospira or scaphoconch (Figs. 4*a–d*) which acts as a float and surrounds the true embryonic shell. The echinospira is transparent, colourless and very thin, and is of a membranous character without lime but more or less hard. In *Lamellaria*, *Trivia* and *Erato* it is firm and keeps its shape more or less perfectly when the animal is dead, but in *Velutina* and *Capulus* it is gelatinous and fairly soft. The British echinospiras have been described and figured recently, except *Capulus* (the larva of *Velutina plicatilis* is unknown); six species are described, *Trivia* (two), *Erato* (one), *Velutina* (one), *Lamellaria* (two), (Lebour, 1936). The echinospiras were at first regarded by the old naturalists as separate genera and were given separate names—*Calcarella*, *Brownia*, etc.; these are now obsolete. All are important in the plankton as they are large; they are powerful swimmers and often abundant. *Lamellaria perspicua*, whose spawn has long been known, bites holes in compound ascidians and lays its eggs therein. Hennedy (1853)* and Peach (1858) described the spawn and the echinospira larvae hatching from them many years ago. The echinospira in all known species of the Lamellariidae is nautiloid, though scarcely perceptible in *Velutina*. The velum is large, bilobed or slightly four-lobed, or six-lobed, and in the late larvae very conspicuous. The true shell lies within the echinospira excentrically, the whorls not corresponding. In *Lamellaria* the mantle grows up round the true shell, enveloping it, the velum disappears, the echinospira shell and operculum are thrown off and the metamorphosed animal crawls, having the appearance of the adult; the change taking place very rapidly. In *Velutina* the mantle does not cover the shell in the adult and the newly metamorphosed young is not much like the parent.

---

* The reference to Hennedy's statement in the *Zoologist* for 1853 could not be confirmed.

Thorson (1935, p. 65) finds that *Velutina undata* from East Greenland has no free-swimming stage but hatches in the crawling stage.

Genus Velutina

Velutina velutina (Müller).

The larvae are described and figured by Lebour (1935*b*, p. 166, pl. iii). The eggs are unknown. It is taken rarely off Plymouth in dredgings. The larva has a slightly nautiloid globular gelatinous echinospira covering of a little more than one whorl, usually more or less covered with minute debris; small dots radiate from near the centre, probably being pores from which mucus exudes. It occurs rather rarely in inshore plankton in late spring and summer. The smallest larva seen was 0·96 mm. across the echinospira. The velum is colourless and bilobed; in late stages it is large with a slight dent in the centre of the margin of each lobe, showing a tendency to be four-lobed. The true shell in later larval stages has about three and a half whorls, with longitudinal ridges (four or five) running outwards from about the middle of the second whorl to the aperture where there is a thick lip. The late larva is about 1·4–2 mm. across the echinospira. The young metamorphosed animal has a shell 1·28 mm. across, with longitudinal ridges still present.

Genus Lamellaria

(Fig. 4*a*)

The echinospira larva of *Lamellaria* is well known and was described and attributed to that genus by Krohn (1855, 1857). Many workers have also described it (Giard, 1875; Pelseneer, 1911; Simroth, 1911; and others). For a description and summary of literature see Lebour (1935*b*). The echinospira is nautiloid with a ridged periphery, the ridges appearing as teeth in side view. The true shell is placed excentrically to the echinospira whorls of which there are several in the later stages. The large velum is at first bilobed and four-lobed, then six-lobed. When ready to metamorphose the mantle rises up round the true shell and the velum, operculum and echinospira shell disappear.

Lamellaria perspicua (L.) (Fig. 4*a*).

The eggs and early larvae are described by Hennedy (1853), Peach (1858), Giard (1875) and Pelseneer (1911). Lebour (1935*b*, p. 164, pl. i) described eggs and all stages up to metamorphosis. Ankel (1935*b*) describes the formation of the egg capsules ("kokons") in detail. The parent lays its eggs in compound ascidians (*Leptoclinum* (= *Trididemnum*), *Polyclinum*, etc.), biting round holes in which the eggs are deposited in capsules, round which the ascidian grows. It is common round our coasts between tide marks and sometimes further out in shallow water. The capsules have a transparent lid through which the eggs, with membrane, can be seen floating in a nutritive fluid. The capsule is about 4 mm. across, and contains many eggs, 0·30 mm. across. According to Giard and Pelseneer some of the developing embryos devour the others (nurse eggs). The newly hatched echinospira is 0·35 mm. across. The velum is bilobed and edged with brown spots. The later larvae have a four-lobed velum which later still becomes six-lobed. The velum has many brown and orange spots and these are also irregularly placed on the other parts of the animal, especially the mantle. Larvae in all stages are found in the plankton throughout the year, especially in spring and summer. This echinospira, *ca.* 2 mm. across at metamorphosis, may be distinguished from the next species by the numerous and fine ridges round the periphery, which in *L. latens* (?) are fewer and coarser.

(?) Lamellaria latens (Möller).

A second species of *Lamellaria* echinospira is common at Plymouth, usually in deeper water which differs from *L. perspicua* in the number and form of the ridges on the echinospira shell and in the colour of the animal which is lighter with fewer dark spots. Also it metamorphoses when the echinospira is about 3 mm. instead of about 2 mm. across. This occurs fairly commonly in the outside plankton and is attributed to *Lamellaria latens*, although the identification is not certain. The larvae are described and figured by Lebour (1935*b*, p. 165, pl. ii).

Family CYPRAEIDAE

(Figs. 3*a*, *b*; 4*c*, *d*)

Two species of *Trivia*, *T. monacha* and *T. arctica*, are now recognized as British. These and *Erato voluta* are the only members of the Cypraeidae (as recognized by early workers) known to have an echinospira larvae. Schiller's new classification, in which he places *Trivia* and *Erato* in the Lamellarioidea as distinct from the Cypraeoidea, which is much more natural, is given above (p. 147), and it is hoped that this will be adopted universally. *Trivia* and *Erato* have a helicoid echinospira shell instead of nautiloid as in *Lamellaria*, but otherwise the larvae are very similar. *Erato* can be distinguished from *Trivia* in having the whorls of the true shell completely separate from those of the echinospira, lying in it excentrically, whilst in *Trivia* the whorls run concurrently. For this reason in *Erato* the echinospira shell is shed complete at metamorphosis, but in *Trivia* the mantle surrounds the echinospira which is absorbed or disappears. In both *Erato* and *Trivia* the young metamorphosed shell has a thin outer lip and remains in this state for some time before the characteristic thickening takes place.

In *Simnia*, which is one of the true species of *Cypraea* (Cypraeoidea of Schilder), the eggs are entirely different, being laid in layers on *Eunicella* (Fig. 2*i*) or *Alcyonium* on which the animal feeds; the larva has no echinospira shell. Macdonald (1859) described and figured a somewhat similar larva belonging to the genus *Pedicularia* from the South Seas. This is closely related to *Ovula* and *Simnia*. Various species of *Cypraea* proper and its close relatives are known to lay masses of eggs in horny capsules which they guard, the newly hatched larva having no echinospira shell.

Genus Erato

Erato voluta (Montagu) (= *E. laevis*).

The larvae are described and figured by Lebour (1933*b*, p. 488, pl. i–ii; 1935*b*, p. 168, pl. vi). The adult is fairly common on the outside dredging grounds. The larva is fairly common in offshore plankton in summer. The eggs are unknown. The echinospira shell is globular and markedly helicoid. The youngest larva seen was 0·64 mm. across the echinospira. It is first very like *Lamellaria* but soon differs in the form. As the larva grows the true shell becomes very excentric. Round the periphery of the echinospira are lines of small dots similar to those described in *Capulus* and in *Velutina*, probably for the passage of mucus. The animal is yellowish with a bilobed velum with a narrow brown border. The velum becomes very large and tends to be slightly four-lobed. Metamorphosis takes place when the echinospira is about 2 mm. across; the mantle covers the true shell when still in the echinospira and when the latter is shed. The larva still keeps the velum for a short period.

Genus Trivia

Trivia monacha (da Costa) (Figs. 3*a*, *b*) (*T. europea* in part in the Plymouth Marine Fauna).

This and the following species were formerly regarded as one under the name of *T. europea*. Pelseneer (1926), who first discovered the eggs, described the animal biting holes in compound ascidians and laying their eggs in them. He also described the newly hatched larva, and, in a later paper (1932), the growth of the young shell to the adult stage. The eggs and larvae are described and figured by Lebour (1931*b*, p. 819, pl. i–iv, as *T. europea*; 1933*a*, p. 477; 1935*b*, p. 168, pl. iv). The eggs were laid in *Diplosoma* and *Botryllus* in the Laboratory. The capsules are flask-shaped, 4·8 mm. across (Figs. 3*a*, *b*), and contain many eggs each covered by a thin membrane and all floating in a common fluid. The newly hatched veliger has an echinospira shell of about one and a half whorls, 0·35 mm. across. The animal is dark; the velum is bilobed with a slight lateral indentation and dark purplish border. The echinospira is ready to metamorphose when it is 1·25 mm. across; it is helicoid, and the whorls of the true shell coincide with the echinospira whorls. The velum grows to a large size. When metamorphosis takes place the mantle rises up and covers both echinospira and true shell, the velum disappearing. The dorsal part of the shell is partially exposed for some time. The shell is smooth and opaque white, with a coiled flat apex and very thin outer lip. The growing mantle is yellowish with purple spots and has papillae at the sides. When full grown the shell lip is thickened. The dorsal part of the shell is coloured with three brown masses, each composed of two parts running together. The whole shell surface is ribbed. The adult is common inshore at Plymouth. Breeding takes place in spring and summer. The larva is fairly common in the plankton.

Trivia arctica (Montagu) (= *T. europea* in part, in Plymouth fauna) (Figs. 4*b*, *c*).

The larvae are described and figured by Lebour (1933*a*, p. 481, pl. i; 1935*b*, p. 168, pl. iv). The adult is common round Plymouth, both inshore with *T. monacha* and offshore. The larvae are fairly common in the plankton in autumn, winter and early spring. Breeding takes place chiefly in winter. This species has probably often been confused with *T. monacha* and recorded as *T. europea*; it has a more northerly distribution. The eggs are not known, but will almost certainly be found to be similar to those of *T. monacha*. The echinospira shell is very like that of *T. monacha*, but the animal is of a much lighter colour. The velum in later stages grows out into four long lobes, bordered by a fine dark line. The smallest larva seen was 0·4 mm. across the echinospira; the largest, ready to metamorphose, was 1·6 mm. across.

Genus Simnia

Simnia patula (Pennant) (Fig. 2*i*).

The eggs and larvae are described by Lebour (1932*a*, p. 107, fig. 1, pls. 1–2). The adult is common at Plymouth among *Eunicella* and *Alcyonium*, on which it feeds and lays its eggs. Young and old larvae are common in the plankton in spring and summer chiefly offshore. Breeding takes place from February to July. The eggs are laid in flat layers in capsules, each capsule containing many eggs. These are pink at first but take on a brown appearance from the developing young whose shells are dark brown. The capsule is about 3·5 mm. across. The egg is about 0·13 mm. across. The newly hatched larva is 0·14 mm. across the shell, with about one and a half whorls; the shell is sculptured with irregular granules, being later reticulated at the edge of the aperture. The velum is bilobed and colourless; later it has four very long lobes. When nearly ready to metamorphose the shell (about 0·8 mm. across) has three and a half whorls and a distinct siphon, and the animal can both swim and crawl. It metamorphoses when the shell is about 0·96 mm. across, the mouth gradually growing round the shell and enveloping the embryonic whorls.

Order STENOGLOSSA

(Figs. 3*f–j*)

This order contains our largest gastropods, which lay, usually, hard and horny egg capsules; the commonest species, such as *Buccinum undatum* (Fig. 3*g*), were familiar to the oldest naturalists. Pelseneer (1910) and others have shown that the hard coverings of these capsules are formed for the main part by glands of the foot, whereas only a few of the Mesogastropoda form them in this way. The eggs are covered by a thin membrane and float in a nutritive layer surrounded by the capsule. The majority of the British Stenoglossa whose developments are known hatch in the crawling stage and are therefore of no importance in the plankton. Some of them, however, have long planktonic stages, such as *Nassarius* and most of the turrids, and there are some of the most important and conspicuous planktonic veligers. The capsules may be laid singly or in masses, rows or clusters, and they may have an infinite variety of form. No instance is so far known of the eggs being in simple gelatinous masses nor of their being shed singly into the sea.

Family MURICIDAE

(Figs. 3*h*, *i*)

So far as is known the egg capsules may be lens-shaped or vase-shaped and may be attached to a substratum by the whole of one surface or by a stalk; they may be laid singly or in clusters. The capsules usually contain several eggs. In some nurse eggs are present. The young, so far as is known, emerge in the crawling stage.

Genus Trophon

Subgenus *Trophonopsis*

Trophon muricatus (Montagu).

Jeffreys (IV, p. 317) describes and figures the egg capsules. They are also described and figured by Lebour (1936, p. 560, pl. iii, figs. 1–4). They are lens-shaped, colourless, transparent and thick-walled and attached by one surface. Each individual lays from two to nine capsules, 2·5 mm. across, containing several eggs, 0·48 mm. across. The young emerge from a thin oval portion at the top of the capsule, spending the veliger stage inside. The animal, with shell 0·64 mm. across and with about one and a half whorls, and still with the velum can be seen in the capsule.

The adult is occasionally dredged off Plymouth. It breeds from February to June.

Genus Nucella

Nucella lapillus (L.) (Fig. 3*h*).

The species is very common on rocks, laying its eggs in simple vase-shaped capsules attached to the rock ledges side by side in layers. It has been well known from the earliest times. Many workers have described the spawn (see Jeffreys, IV, p. 275). The capsule is 8–9 mm. high and about 2 mm. across, and attached by a wide flat base with a thin stalk supporting a narrow oval vase; it is hard and yellowish, brown or purple, but usually pale yellow; the top narrows and covers over thinly at the point where the young eventually emerge. Some hundreds of eggs float inside in a fluid; about 15–25 of these hatch out, the remainder being eaten (nurse eggs) by their neighbours. The young remain in the capsule until the crawling stage. The newly hatched young has a smooth whitish yellow shell with about two whorls. The species breeds throughout the year.

Lamy (1928) describes egg capsules of several other forms closely related to *Nucella* and very similar.

Genus Urosalpinx

Urosalpinx cinerea (Say).

This species has recently been introduced into British waters, living chiefly on the oyster beds. It is now included in the British fauna, being found in abundance in the Mersey Estuary. The egg capsules are vase-shaped, and laid in clusters on shells or stones; each is attached by a flat base, and has a thickish stalk supporting the vase. The capsule is 8 mm. high, about 4 mm. thick in the widest part, angulated, horny and hard, and yellowish in colour; it contains several eggs, 0·24 mm. across. The young hatch in the crawling stage, and are somewhat purplish. Breeding takes place in summer (information kindly supplied by Prof. J. H. Orton). The capsules are figured and described by Orton (1929).

Genus Ocenebra

Ocenebra erinacea (L.) (Fig. 3*i*).

Jeffreys (IV, p. 309) describes the egg capsules. This species is common on our shores on the rocks and under stones between tide marks and beyond. Its eggs are laid in clusters in the rock crevices or on stones and shells and are somewhat similar to those of *Nucella* but angular, and having much fewer eggs and no nurse eggs. The young emerge in the crawling stage. The capsule is yellowish, about 10 mm. high, and hard and horny; it is fixed by a flat base and a narrow stalk supports the vase which is somewhat flattened on one surface and rounded on the other with three keels which make the section triangular. Each capsule contains from 12 to 20 eggs, all of which usually develop. Breeding takes place in late spring and summer. The newly hatched young are 0·96 mm. long, with the beginning of a siphon; the shell is smooth with about two and a half whorls, the edge beginning to be crenulated.

Family BUCCINIDAE

(Fig. 3*g*)

The eggs are laid in horny capsules, either singly or several together, usually attached to some substratum or to one another, and sometimes forming large masses. The capsule is more or less lens-shaped, the opening for the young to emerge being at the side or base. Nurse eggs are often present, and one capsule may contain hundreds of eggs of which only a few hatch. In all instances known the young emerge in the crawling stage with usually several whorls. Thorson (1935) gives descriptions of the eggs and young of several species from East Greenland.

Genus Liomesus

Liomesus ovum (Turton).

Jeffreys (IV, p. 299) describes and figures the egg cases (as *Buccinopsis dalei*) as sometimes deposited on the under side of the maternal shell; the base is narrower than the upper portion. This is not the *Tritonium ovum* of Middendorff (=*Buccinum ovum* Midd. of Thorson, p. 34).

Genus Beringius

Beringius turtoni (Bean).

The egg capsules are described by Howse (1847 as *Fusus turtoni*), and quoted by Jeffreys (IV, p. 332): "Eggs pale orange, either solitary or two together and attached side by side, not to each other, but to a rather broad membranous substratum, they are triangularly oval, the base being the narrowest part and consisting of an outer filmy sheath and an inner and thick fibrous case, the latter resembles in structure a coconut husk, the opening is a wide slit at the top. Six fry in one capsule. Fry almost cylindrical and of a dark reddish brown hue."

Genus Volutopsius

Volutopsius norwegicus (Gmelin).

The egg capsules are described and figured by Howse (1847, p. 162, pl. x, fig. 3, as *Fusus norwegicus*). The capsules were first noticed by Mr King (Jeffreys, IV, p. 331), solitary, forming a compressed hemisphere, about an inch in diameter, dirty lemon colour, semi-transparent, attached by the whole of its base to the inside of old bivalve shells and other flat substances and edged by a rim or strip of membrane. The upper surface is covered with a thin whitish coat, which breaks up into crystalline particles and is finely corrugated. The underside is satiny. The ova are pink or bright flesh-colour. There are 2 to 4 perfect "fry" in each capsule which escape through a slit in the rim. Thorson (1935, p. 23, fig. 18) shows an almost more than subhemispherical capsule from East Greenland, which is dull, yellowish cream colour, slightly tuberculated and fairly transparent. The base is 28–30 mm. It only contained immature eggs. Friele (1882) and Dons (1913) also mention the capsules.

Genus Colus

Colus islandicus (Gmelin).

The only British record occurs off the Shetlands. Thorson (1935, p. 13, figs 5–7 as *Sipho*) describes the eggs and young, the egg capsules having been previously described by Friele (1882). The capsule is light yellow, lens-shaped, slightly domed, and attached by a flat base to some substratum, usually stones. A medium-sized capsule has a basal diameter of 13 mm. with 7350 eggs. Only one to five embryos usually develop, the rest being eaten (nurse eggs); once 16 were found, but there were generally three. The smallest capsule had a basal diameter of 1·5–1·75 mm. The apex is oblique. The largest embryo before emerging is 8·5 mm. (only one embryo in capsule with base 12 mm.) and has three and a half whorls, a little more than half a whorl being spirally sculptured as in the adult. On the occasion when there were 16 embryos in a capsule, 15 mm. at base, the young emerged with one and a half to two whorls and a length of 3·5 mm. The size of the young depends on the number of nurse eggs per embryo.

Colus gracilis (da Costa).

The egg capsules are described by Jeffreys (IV, p. 337 as *Fusus*) "solitary, small, membranous, pouch-shaped and attached by a broad base to stones and corallines: this surface is microscopically and closely reticulated; orifice extremely large, and sometimes having the edge partly stained with pink. Each capsule contains only a single embryonic shell, which is transparent, and through it may be seen the orange liver and two unequal-sized plumes of pale yellow gills."

Subgenus *Siphonorbis*

Colus howsei (Marshall).

Jeffreys (IV, p. 339 as *Fusus propinquus*) describes the egg capsules as "solitary and attached to the inside of old bivalves; they are hemispherical, and resemble those of *F. gracilis*, but have a smaller and oval orifice; the base is margined by a narrow membrane. Embryo the colour of a pomegranate."

Colus jeffreysianus (Fischer).

Jeffreys (IV, p. 341) describes the "fry" (as *Fusus buccinatus*) as "distinct from that of *F. propinquus* as the adult of each from one another".

Genus Neptunea

Neptunea antiqua (L.).

Jeffreys (IV, p. 327, pl. iv, fig. 3) describes and figures the spawn (as *Fusus antiquus*) and states that it has been well described by Baster (1762) in his "Opuscula subseciva". "Egg cases or capsules overlap one another in an imbricated fashion, each being firmly attached by its base to the underlying capsule." They are also described and figured by Meyer and Möbius (1872):

"They are deposited in clusters of from a dozen to a hundred, the capsules in each cluster being equal in size. Those which compose one cluster, however, are not half as large as those forming another cluster, although in both cases the fry are in the same state of maturity. When they are dry, the upper or convex side shrivels, and is wrinkled and pitted; the under or flat side (which by contraction becomes concave) is of a silky texture, and divided across by a few lines; the opening is a wide slit, lying just under the top which makes a narrow flap. Before leaving the capsule the fry are perfectly formed, with conspicuous tentacles, eyes and operculum. The shell has two whorls, the first being smooth and the others showing a few incipient striae. Each capsule produces only from 2 to 4 fry. The latter end of winter seems to be the spawning season."

Genus Buccinum

Buccinum undatum (L.) (Fig. 3*g*).

Baster (1762) and many other early writers have investigated the spawn. It is figured in Ellis's *Corallines* as *Alcyonium* and *Vesicularia marina* of Bauhm, and by Fischer (1887, p. 92) and among others in the *Plymouth Aquarium Guide* (1935, p. 39). They are called "sea-wash" balls because they are used by sailors to wash their hands. Dr Johnston compares the egg mass to the nest of a bumble-bee (very appropriate). Jeffreys (IV, p. 291) describes the spawn: "it is composed of numerous cartilaginous pouches (in reality of chitin), of the shape and size of a large split pea, piled irregularly one upon another, and attached to their edges at the base....Each cell contains at first several hundred eggs, which are afterwards so greatly reduced in number that only from 15 to 30 fry come to maturity." The spawning season is between October and May according to locality. The young emerge in the crawling stage with about two and a half whorls. The shell is smooth, beginning to be spirally striated on the outer whorl, and the shell siphon is beginning to be formed. The newly hatched young are about 1 mm. long.

Buccinum humphreysianum Bennett.

Jeffreys (IV, p. 395) states that the egg cases are separate and hemispherical. Thorson (1935, pp. 24–35) describes the spawn of five species from East Greenland, all being very similar to those of *B. undatum* and all hatching in the crawling stage.

Genus Chauvetia

Chauvetia brunnea (Donovan) = *Syntagma brunnea* in Plymouth Marine Fauna.

At Plymouth, spawn cases were found in the plunger jars inhabited by this species, but without eggs. The capsules were similar to those of *Philbertia*, being lens-shaped, colourless and transparent; they were attached to the glass by the flat under surface, the upper part being rounded with a very thin portion in the centre.

Family NASSARIIDAE

(Fig. 3*j*)

The egg capsules are more or less flattened and horny, flask-shaped or irregularly vase-shaped. They are laid singly, or in rows, or scattered irregularly in masses, attached to some substratum, stones, shells, Bryozoa, Hydrozoa or Algae. No nurse eggs are known, all the eggs in a capsule usually developing. There are many eggs in each capsule, with membranes, and floating together in a fluid within the capsule. The capsule is usually attached to the substratum by a flattened base, a narrower portion bearing the flask, which is inflated, usually narrowing at the top and closed with a thin covering which is broken when the eggs emerge. All the species whose young are known hatch as free-swimming veligers, some remaining for a long time in the plankton.

Genus Nassarius

Subgenus *Hima*

Nassarius reticulatus (L.).

The egg capsules are described and figured by Jeffreys (IV, p. 348) as *Nassa*; Pelseneer (1911) describes the eggs and larvae up to the time of hatching and figures the developing embryos. He also (1906) figures the egg capsule and larval shell. Ankel (1929) has investigated the laying of the egg capsule and gives photographic illustrations. The capsules are well-known objects, often seen in rows on the leaves of *Zostera*. The eggs and larvae are described and figured by Lebour (1931*a*, p. 797, fig. 1, pl. i, figs. 1–2, pl. ii and iii) and the whole life history was followed. The adult is common on our coasts, the larvae being very common in the coastal plankton throughout the year but especially in spring and summer. The capsule is pale horn colour, hard, rounded on one flattened surface and almost flat on the other, vase-shaped, fixed by a flat base, then narrowing and enlarging again into the vase; it is 4·8–5 mm. high, and about 4 mm. across, containing about 50, or less, to 100 eggs, 0·16 mm. across, all of which usually develop. The newly hatched larva is free-swimming, about 0·28–0·30 mm. across the shell with about one and a half whorls. The velum is bilobed with a reddish brown border. The outer lip of the shell projects into a conspicuous process. The late larva has a slight constriction in the velar lobes, making them tend to be four-lobed. When the shell is 0·72–0·8 mm. across with three whorls it metamorphoses, the shell canal having been formed earlier and the animal both swimming and crawling.

Nassarius incrassatus (Ström) (Fig. 3*j*).

The eggs and larvae are described and figured by Lebour (1931*a*, p. 797, figs. 2 and 3, pl. iv and v). They are much like those of *N. reticulata* but smaller. The capsules are usually laid in clusters but sometimes a few in a row, on Bryozoa, hydroids or weeds. Fischer (1892) was the first to describe the capsules. The capsule is 1·5–2 mm. high, containing several eggs, 0·16 mm. across. The newly hatched larva has a shell 0·18–0·02 mm. across, with one and a half whorls; the velum is bilobed, at first being colourless, and later having a brown border. In a few days the velum develops four lobes which later grow very long, each with a brown spot at the end. The larvae are ready to metamorphose with a shell 1·5 mm. high; they can both crawl and swim. The adults are very common on the shore and below low-water mark. The larvae are very common in the inshore plankton and sometimes also in the offshore waters, the late stages being found much farther out than those of *N. reticulatus*. Breeding takes place chiefly in spring and summer, but occasionally larvae may be found in any month of the year. It is one of the most important planktonic veligers.

Nassarius pygmaeus (Lamarck).

Although this is a British species, its eggs and young have not been seen here. Vestergaard (1935, p. 218, figs. 1, 3) has described them from North-east Jutland, occurring at a depth of 20–25 metres, one capsule being on a *Delesseria* and four on the shell of a living specimen of *Aporrhais pespelicani*. The capsules were solitary, 2·5 mm. high and 1·5 mm. broad, thus being slightly larger than those of *N. incrassatus*; they were also similar in shape but rather rounder with a broader base, containing 40–50 eggs which hatched out. The newly hatched larva had a shell 0·2 mm. across with rather more than one whorl and a small process on the outer lip. The velum was bilobed, the lobes being rounded, and bordered with red-brown. A later stage, almost certainly belonging to this species, has a shell about 1 mm. high, with a radial sculpture; the outer aperture has a tooth-like process as in the other *Nassarius* larvae; the velum is large and four-lobed.

Egg capsules of other *Nassarius* species from different countries are described and resemble those of the British species (Tryon, 1881), *Nassa obsoleta* has much corrugated capsules but similarly shaped (Ankel, 1929).

Family TURRIDAE

(Figs. 3*f*; 4*g*)

The egg capsules, so far as is known, are lens-shaped, solitary, and attached by the whole of the flattened base to some substratum. In the centre of the free convex surface is the exit hole covered by a thin membrane. The embryonic whorls of the adults which represent the larval shells are sharply differentiated into two groups, those with smooth apices (*Haedropleura*, *Lora*, *Mangelia*) and those with reticulated or elaborately sculptured apices (*Philbertia*).

In all British species known the larva hatches as a veliger, but Thorson (1935, p. 36) has described and figured from East Greenland the spawn and young of five species of *Bela* (=*Lora* of Winckworth) including *B. trevelyana* Turton = *Lora trevelliana* Turton of Winckworth, which is also a British species. Its spawn and young have not yet been identified in British waters. In all the East Greenland species Thorson found that the young emerged in the crawling stage. The British species whose developments are known have a long veliger stage and are important members of the plankton. Verrill (1882) has observed similarly shaped capsules belonging to several species of *Bela* from New England. Larvae which are probably *Haedroplura septangularis* are described and figured by Lebour (1936, p. 562, pl. iii, figs. 8–18).

Genus Lora

Lora turricula (Montagu).

Breeding is unknown in British waters, but Vestergaard (1935, p. 218, figs. 1, 2) has described the capsules and newly hatched young from Frederikshavn, Denmark (as *Bela*). The capsule has two ridges running from the centre and dividing its surface into halves. The newly hatched young have a smooth shell and a large velum with large pigment spots not unlike those of *Mangelia* (see below).

All the species of *Bela* described by Thorson have similar ridges on the capsule, and the capsule of *Philbertia gracilis* from Plymouth (see below) are also divided, but in *Mangelia nebula* and *Philbertia linearis* these ridges or divisions were not seen.

An unknown turrid larva, probably belonging to the genus *Lora*, has been described and figured by Lebour (1936, p. 563, pl. iii, figs. 19, 20).

Genus Mangelia

The only egg capsules known belonging to this genus are those of *Mangelia nebula* which are very like those of *Philbertia*, and of *Bela* described by Thorson but without the ridges. The capsules are quite smooth. The larvae of *Mangelia nebula* are very striking veligers remaining for a long time in the plankton and having a very large velum decorated with spots in a similar way to that of *Lora turricula* described by Vestergaard in the young larva; but in the older larva the velum hangs over the shell like a true veil. A second late larva which metamorphosed in captivity is described and figured by Lebour (1936, p. 563, pl. iii, figs. 5–7) which is very similar to that of *Mangelia nebula* but slightly larger and with very faint striae on the apex. This has been attributed provisionally to *M. coarctata*, the only other species of *Mangelia* known from Plymouth; although having an operculum in the metamorphosed form the identification is somewhat doubtful.

Subgenus *Bela*

Mangelia nebula (Montagu).

The eggs and larvae are described and figured by Lebour (1934*b*, p. 547, pl. ii). The adult is common in Plymouth Sound and sometimes outside in shallow water. The larvae are common in the plankton, both in inshore and offshore waters. The egg capsules are lens-shaped, smooth and transparent, 1·6 mm. across, containing about 60 eggs, 0·16 mm. across. Even before the larva leaves the egg the velum is large and ornamented with conspicuous orange spots. The shell of the newly hatched larva is smooth and 0·23 mm. across; the velum is bilobed. Later larvae have a very large velum which may completely cover the shell, and the last whorl of the shell begins to be tuberculated; the siphon is conspicuous. The shell is 0·96–1 mm. long with three and a half to four whorls when ready to metamorphose. The base of the foot is pale grey, otherwise the animal is colourless. Breeding takes place in summer.

Genus Philbertia

(Figs. 3*f*; 4*g*)

So far as is known the larvae of this genus closely resemble one another, the shells being conspicuously sculptured and attaining a large size before losing the velum which is bilobed or four-lobed and usually large. The capsules are of the usual turrid form, with or without ridges.

Subgenus *Comarmondia*

Philbertia gracilis (Montagu).

The eggs and larvae are described and figured by Lebour (1933*c*, p. 507, pl. i, 1934*b*, p. 550, pl. iv, fig. 6). The adult is dredged fairly commonly usually outside Plymouth Sound. Larvae are fairly common in the plankton in spring and summer. The capsules are 3·4 mm. across with ridges dividing them across on the surface; they are coarsely reticulated and contain about 40–80 eggs, 0·16 mm. across. The young remain long in the capsule and before hatching have a large slightly bilobed velum with heavy brown pigment and the shell siphon already formed. The newly hatched larval shell is 0·24–0·80 mm. long, the size varying with the number of eggs in the capsule, as was found by Thorson (1935) in many of the East Greenland prosobranchs. One capsule contained 40 young, 0·80 mm. long. The shell aperture is drawn out externally into a process; the velum at first slightly four-lobed with a large amount of brown pigment, later develops very long lobes (Fig. 4*g*). The shell is dark brown, heavily sculptured with irregular dots and flecks on the first two to two and a half whorls, the later whorls keeled with oblique striations. There are large orange and brown spots on the velar lobes. The animal is yellowish and can swim or crawl when the shell is 1·76 mm. long with four and a half whorls and then it metamorphoses. It is important in the plankton.

Subgenus *Philbertia*

From the apices of all the species known which are sculptured in a characteristic way it can be seen that the larval shell has several whorls before metamorphosis and that the shell is always reticulated, the first one and a half whorls with straight reticulations, which in the later whorls are oblique. It is the same with the subgenus *Teres* and probably with many others of the genus, but the sculpture is quite different from that of *Comarmondia* and the apices sharply differentiated from *Mangelia* and *Lora*. The velum in all those known is colourless and bilobed to four-lobed, the lobes rounded and not large. Jeffreys (IV, p. 366) has noted the sculpture of several species, and this characteristic sculpture is well known to palaeontologists and systematists generally.

Philbertia leufroyi (Smith).

Jeffreys (IV, p. 366) notes the apex (as *Defrancia*). The eggs are not known. The larvae are described and figured by Lebour (1934*b*, p. 553, pl. iv, figs. 1, 2, 4, 8). They are very like those of *P. linearis* (see below) but with fewer whorls and broader; the velum is rather larger; the animal is very similar, having three and a half whorls in the embryonic shell and being pinkish brown to deeper brown. It is not uncommon in the plankton in spring and summer. The late veliger has a shell 0·70–0·80 mm. high.

Philbertia purpurea (Montagu).

Jeffreys (IV, p. 273) notes the sculpture and embryonic whorls (as *Defrancia*), also Lebour (1934*b*) notes three whorls.

Philbertia asperrima (Brown).

Jeffreys (IV, p. 371) notes the sculpture of the embryonic shell (as *Defrancia reticulata*). The late larvae are described together with the embryonic whorls by Lebour (1934*b*). The larva is very similar to that of *Philbertia linearis*, the embryonic shell having four and a half whorls with very irregular reticulations, and being of a lighter colour.

Philbertia linearis (Montagu).

Jeffreys (IV, p. 369) (as *Defrancia*) has described the egg capsules and newly hatched young, and also the sculpture of the embryonic whorls. His measurements of the capsules do not agree with those from Plymouth and may refer to a different species. The eggs and larvae are described by Lebour (1934*b*, p. 550, pl. iii, figs. 1–6, pl. iv, figs. 3, 5, 7). The adult is fairly common in dredgings from the Sound and occasionally outside. The larvae are common in the inshore and offshore plankton in spring and summer, rarely in autumn. Capsules were laid in the Laboratory in February and March; they were 1·5 mm. to 2 mm. across, without ridges, and containing 60–80 eggs, 0·14–0·15 mm. across. The larvae did not hatch out, but all stages are to be found in the plankton. There is a dark reticulated shell. The velum is colourless, bilobed at first, later developing four-lobes; the lobes are round and short. The youngest larva seen was 0·19 mm. across with one and a half whorls; the outer lip was produced. In the late larva the shell is 0·80 mm. long with four whorls, when it is ready to metamorphose.

Subgenus *Teres*

Philbertia teres (Reeve).

Jeffreys (IV, p. 262) notes the sculpture of the embryonic whorls (as *Defrancia*), as does also Lebour (1934*b*, pl. iii, figs. 8–20). The late larva has four whorls.

REFERENCES

ADAMS, A., 1857. A new species of *Macgillivrayia*. *Ann. Mag. Nat. Hist.*, Ser. 2, Vol. XIX, pp. 373–4.

—— 1861. On a supposed new genus and on some new species of pelagic Mollusca. *Ann. Mag. Nat. Hist.*, Ser. 3, Vol. VIII, pp. 401–4.

ANKEL, W. E., 1929. Über die Bildung der Eikapsel bei Nassa-Arten. *Zool. Anz.* Supp. 4 (*Verh. d. Deutsch. Gesellsch. E. V. auf der* 33. *Jahresversammlung zu Marburg*), pp. 219–30.

—— 1930. Nähreierbildung bei *Natica catena* (da Costa). *Zool. Anz.*, Bd. 89, pp. 129–35.

—— 1935*a*. Die Pantoffelschnecke, ein Schädling der Auster. *Natur und Volk*, Vol. 65, pp. 173–6.

—— 1935*b*. Das Gelege von *Lamellaria perspicua* L. *Zeitschr. Morphol. Ökologie Tiere*, Bd. 30, Heft 4, pp. 635–47.

BASTER, J., 1762–65. *Naturkundige Uitspanningen*. Te Haarlem by J. Bosch.

BOAS, J. E. V., 1886. Bidrag til Pteropodernes Morfologi og Systematik samt til Kundskaben om deres geografiske Udbredelse. Spolia Atlantica. *Kgl. Dansk. Vid. Selsk. Skr.* (6), Vol. IV, No. 1, 231 pp.

LO BIANCO, S., 1888. Notizie biologiche riguardante specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. *Mitt. Zool. Stat. Neapel*, Vol. VIII, pp. 385–440.

—— 1899. Notizie biologiche riguardante specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. *Mitt. Zool. Stat. Neapel*, Vol. XIII, pp. 448–573.

BOUTAN, L., 1885. Recherches sur l'Anatomie et le Développement de la Fissurelle. *Arch. Zool. Exp. Gén.*, 2^e Sér., T. III *bis*. Suppl., 4^e Mém. pp. 1–173.

—— 1898. Sur le développement de l'*Acmaea virginea*. *C.R. Acad. Sci. Paris*, CXXVI, pp. 1887–9.

—— 1899. La cause principale de l'asymétrie des mollusques gastéropodes. *Arch. Zool. Exp. Gén.*, 3^e Sér., Vol. VII, pp. 203–342.

CAULLERY, M. & PELSENEER, P., 1910. Sur la ponte et le développement du Vignot (*Littorina littorea*). *Bull. Sci. France Belgique*, T. XLIV, pp. 357–60.

CONKLIN, E. G., 1891. Preliminary Note on the Embryology of *Crepidula fornicata* and of *Urosalpinx cinerea*. *Johns Hopkins University Circulars*, Vol. 10, No. 88, pp. 89–90.

—— 1897. The embryology of *Crepidula*. A contribution to the cell lineage and early development of some marine gastropods. *Journ. Morph.*, Vol. XIII, No. 1, pp. 1–226.

COOKE, A. H., 1895. Molluscs. In the *Cambridge Natural History*, III, pp. 1–459.

CROFTS, D. R., 1929. *Haliotis*. *L.M.B.C. Memoirs*, XXIX, pp. 1–174.

CRAVEN, A. E., 1877. Monographie du genre *Sinusigera*. *Ann. Soc. Malac. Belgique*, Vol. XII, p. 112.

—— 1883. On the Genus *Sinusigera* d'Orb. *Ann. Mag. Nat. Hist.*, Ser. 5, Vol. XI, pp. 141–2.

DAVIS, J. R. AINSWORTH & FLEURE, H. J., 1903. *Patella*. *L.M.B.C. Memoirs*, X, pp. 1–76.

DELSMAN, H. C., 1914. Entwicklungsgeschichte von *Littorina obtusata*. *Tijdschr. Nederl. Dierkundige Vereeniging*, Ser. 2, Deel 13, pp. 170–340.

DONS, C., 1913. Om eggloegningen hos enkelte Buccinider Zoologiske notiser. II. *Tromsø Museums Aarshefter*, 35–36.

FISCHER, H., 1892. Recherches sur la Morphologie du Foie des Gastéropodes. *Bull. Sci. France Belgique*, XXIV (4), Vol. III, pp. 260–346.

FISCHER, P., 1880–87. *Manuel de Conchyliologie.*

FLATTELY, F. W. & WALTON, C. L., 1922. *The Biology of the Sea-Shore*. Pp. 1–334. London.

FRIELE, H., 1882. *The Norwegian North-Atlantic Expedition*, 1876–78. Mollusca, 1–2 (pt. 1, pp. 38; pt. 2, pp. 44).

GERSCH, M., 1936. Der Genitalapparat und die Sexualbiologie der Nordseetrochiden. *Zeitsch. Morph. Ökologie Tiere*, Bd. 31, Heft 1, pp. 106–50.

GIARD, A., 1875. Sur l'Embryologie du *Lamellaria perspicua*. *C.R. Acad. Sci. Paris*, T. LXXX, pp. 736–9.

—— 1885–6. Synopsis de la Faune Marine de la France Septentrionale (Suite 1). *Bull. Sci. Département du Nord*, No. 5–6 (1886), pp. 157–78.

HENKING, H., 1894. Beiträge zur Kenntnis von *Hydrobia ulvae* Penn. und deren Brutpflege. *Ber. naturf. Ges. zu Freiburg i. B.* VIII, pp. 89–110.

HERDMAN, W., 1888–9. Note in Second Annual Report of the Liverpool Marine Biological Station on Puffin Island. *Proc. Liv. Biol. Soc.* III, 1888–9.

HERTLING, H., 1928. Beobachtung und Versuche an den Eiern von *Littorina* und *Lacuna*. Bedeutung der Eihüllen. *Wiss. Meeres. Komm. Unt. deutsch. Meere*, N.F., Abt. Helgoland, Bd. XVII, 2, 49 pp.

—— 1932. Zur Kenntnis des Laichbandes und der Veligerlarven von *Natica pulchella* Risso. *Zool. Anz.*, Bd. 100, pp. 95–100.

HERTLING, H. & ANKEL, W. E., 1927. Bemerkungen über Laich und Jugendformen von Littorina und Lacuna. *Wiss. Meeres. Komm. Unt. deutsch. Meere*, N.F., Abt. Helgoland, Bd. XVI, 7, 13 pp.

HOWSE, R., 1847. Notes on a Dredging Excursion off the Coast of Durham, with Descriptions of the Ova-capsules of *Fusus norvegicus* and *F. turtoni*. *Ann. Mag. Nat. Hist.*, Vol. XIX, pp. 160–4.

JEFFREYS, J. G., 1863–9. *British Conchology*, Vol. II, 1863; Vol. III, 1865; Vol. IV, 1867; Vol. V, 1869.

KROHN, A., 1853. Über einen neuen, mit Wimpersegeln versehenen Gasteropoden. *Arch. Naturgesch.* XIX. Jahrg. pp. 223–5.

—— 1855. Nachtrag zu dem Aufsatze über die *Echinospira diaphana*. *Arch. Naturgesch.* XXI. Jahrg. pp. 1–5.

—— 1857. Fernere Nachträge zu dem Aufsatze über *Echinospira* nebst Beobachtungen über eine ihr verwandte Larve. *Arch. Naturgesch.* XXIII. Jahrg. pp. 252–61.

LAMY, E., 1928. La Ponte chez les Gastéropodes prosobranches. *Journ. Conchyliologie*, Vol. LXXII, pp. 25–52, 80–126.

LEBOUR, M. V., 1931*a*. The larval stages of *Nassarius reticulatus* and *Nassarius incrassatus*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, No. 3, pp. 797–818.

—— 1931*b*. The larval stages of *Trivia europea*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, No. 3, pp. 819–32.

—— 1932*a*. The larval stages of *Simnia patula*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, No. 1, May, pp. 107–15.

—— 1932*b*. The eggs and early larval stages of two commensal gastropods, *Stilifer stylifer* and *Odostomia eulimoides*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 117–22.

—— 1933*a*. The British species of *Trivia*: *T. arctica* and *T. monacha*. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, No. 2, Jan., pp. 477–84.

LEBOUR, M. V., 1933*b*. The larval stages of *Erato voluta* (Montagu). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, No. 2, pp. 485–90.

—— 1933*c*. The life-histories of *Cerithiopsis tubercularis* (Montagu), *C. barleei* Jeffreys and *Triphora perversa* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, No. 2, pp. 491–8.

—— 1933*d*. The eggs and larvae of *Turritella communis* Lamarck and *Aporrhais pes-pelicani* (L.). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, No. 2, pp. 499–506.

—— 1933*e*. The eggs and larvae of *Philbertia gracilis* (Montagu). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, No. 2, pp. 507–10.

—— 1933*f*. The importance of larval Mollusca in the plankton. *Journ. Cons. Int. Expl. Mer*, Vol. VIII, No. 3, pp. 335–43.

—— 1934*a*. Rissoid larvae as food of the young herring. The eggs and larvae of the Plymouth Rissoidae. *Journ. Mar. Biol. Assoc.*, Vol. XIX, No. 2, May, pp. 523–39.

—— 1934*b*. The eggs and larvae of some British Turridae. *Journ. Mar. Biol. Assoc.*, Vol. XIX, No. 2, May, pp. 541–554.

—— 1935*a*. The echinospira larvae of Plymouth. *Proc. Zool. Soc. London*, pp. 163–74.

—— 1935*b*. The breeding of *Littorina neritoides*. *Journ. Mar. Biol. Assoc.*, Vol. XX, No. 2, Aug., pp. 373–8.

—— 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XX, No. 3, pp. 547–65.

LINKE, O., 1933*a*. Morphologie und Physiologie des Genitalsapparates der Nordseelittorinen. *Wiss. Meeres. Komm. Unt. deutsch. Meere in Kiel und der Biol. Anst. Helgoland*, N.F., Helgoland, Bd. XIX, 5, 60 pp.

—— 1933*b*. Der Laich von *Skeneopsis planorbis* O. Fabricius (Gastrop. Prosobranch.). *Zool. Anz.*, Bd. 103, Heft 11/12, pp. 207–11.

—— 1935. Der Laich von *Littorina* (*Melaraphe*) *neritoides* (L.). *Zool. Anz.*, Bd. 112, Heft 3/4, pp. 57–62.

LOVÉN, H., 1839. Bidrag till Känmadomen af Molluskernas utveckling. *Kongl. Vetenskaps-Akademien Handlingar Stockholm för år* 1839, pp. 227–41.

—— 1844. Om Nordiska Hafs-Mollusken. *Öfversight af Kongl. Vetenskaps-Akademien Förhandlingar Stockholm första årgången*, pp. 48–53.

LUND, A., 1834. Recherches sur les enveloppes d'œufs des Mollusques gastéropodes pectinibranches. *Ann. Sci. Nat.*, S. 2, Zool., T. 1, pp. 84–112.

MACBRIDE, E. W., 1914. *Text-book of Embryology*, Vol. 1, Mollusca, pp. 291–371.

MACDONALD, J., 1855. Note in *Ann. Mag. Nat. Hist.*, Ser. 2, Vol. XVI, pp. 206–7 (*Proc. of Learned Societies*, April 26).

MACDONALD, J. D., 1859. On the probable metamorphosis of *Pedicularia* and other forms. *Trans. Linn. Soc. London*, Vol. XXII, pp. 241–3.

—— 1860. Further observations on the metamorphosis of Gasteropoda. *Trans. Linn. Soc. London*, Vol. XXIII, pt. 1, pp. 69–82.

MEYER, H. A. & MÖBIUS, K., 1872. *Fauna der Kieler Bucht*, Bd. 2, Die Prosobranchia und Lamellibranchia, pp. i–xxiv, 1–139.

MILNE-EDWARDS, H., 1832. In Audouin & Milne-Edwards. *Recherches Hist. Nat. litt. France.*

MOORE, H. B., 1937. The biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life and mortality. *Journ. Mar. Biol. Assoc.*, Vol. XXI, No. 2, pp. 721–42.

MOORHOUSE, F. W., 1932. Notes on *Trochus niloticus*. *Great Barrier Reef Expedition*, 1928–29. *Scientific Reports*, Vol. III, No. 5, British Museum (Natural History), pp. 145–55.

ODHNER, N. H., 1914. Notizen über die Fauna der Adria bei Rovigno. Beiträge zur Kenntnis der marinen Molluskenfauna von Rovigno in Istrien. *Zool. Anz.*, Bd. 44, pp. 156–70.

ORTON, J. H., 1912–13. An American enemy of the English oyster farmer. *Trans. Plymouth Institution*, pp. 247–61.

—— 1928. Observations on *Patella vulgata*. Part I. Sex phenomena, breeding and shell-growth. *Journ. Mar. Biol. Assoc.*, Vol. XV, No. 3, pp. 851–74.

ORTON, J. H. & AMIRTHALINGAM, C., 1929. The oyster drills on English oyster beds. *Nature*, Vol. CXXIV, Aug. 24, pp. 298–9.

PATTEN, W., 1886. The embryology of *Patella*. *Arb. Zool. Inst. Wien*, Bd. VI, pp. 149–74.

PEACH, C. W., 1858. A few remarks on *Lamellaria tentaculata* and its nidification, etc., as observed at Wick. *Proc. Roy. Phys. Soc. Edinburgh*, Vol .I, pp. 455–8.

PELSENEER, P., 1894. *Introduction à l'étude des Mollusques*, pp. 1–217. Bruxelles.

—— 1906. Mollusca in *A Treatise on Zoology*, edited by E. Ray Lankester, Part V, pp. 1–355.

—— 1910. Glandes pédieuses et coques ovigères des Gastropodes. *Bull. Sci. France Belgique*, T. XLIV, pp. 1–9.

—— 1911. Recherches sur l'embryologie des Gastropodes. *Mém. Acad. Royale Belgique*, 2^e^ Sér., T. III, pp. 1–167.

—— 1926. Notes d'Embryologie malacologique. Ponte et développement de *Cypraea europea*, *Triforis perversa* et *Lucina lactea*. *Bull. Biol. France Belgique*, T. LX, pp. 88–112.

—— 1932. La métamorphose préadulte des Cypraeidae. *Bull. Biol. France Belgique*, T. LXVI, 2, pp. 149–63.

POWELL, A. W. B., 1930. New species of New Zealand Mollusca from shallow-water dredgings. *Trans. and Proc. N.Z. Inst.*, Vol. 60, Part 4, pp. 532–43.

ROBERT, A., 1902. Recherches sur le Développement des Troques. *Arch. Zool. Exp. Gén.*, 3^e^ Sér., X, pp. 269–538.

SCHILDER, F. A., 1936. Anatomical characters of the Cypraeacea which confirm the conchological classification. *Proc. Malacol. Soc.*, Vol. XXII, Part II, pp. 75–112.

SIMROTH, H., 1895. Die Gastropoden der Plankton-Expedition. *Erg. d. Plank. Exp. der Humboldt-Stiftung*, Bd. II, F.d. pp. 1–206.

—— 1896–1907. Mollusca in Bronn's *Tierreich*, Bd. III, Abt. II, Gastropoda Prosobranchia, pp. 628–720.

—— 1911. Die Gastropoden des Nordischen Planktons. *Nordisches Plankton*, V, pp. 1–36.

SMITH, F. G. W., 1935. The Development of *Patella vulgata*. *Phil. Trans. R. Soc. London*, Ser. B, *Biol. Sci.* No. 520, Vol. 225, pp. 95–125.

STEPHENSON, T. A., 1924. Notes on *Haliotis tuberculata*. *Journ. Mar. Biol. Assoc.*, Vol. XIII, No. 2, pp. 480–95.

TATTERSALL, W. M., 1908. *British Association Reports*, Dublin, p. 746; *Nature*, Vol. 78, Oct. 22, 1908, p. 649.

—— 1910. *Athenaeum*, Feb. 13, pp. 203–4, and at the Challenger Society, Jan. 1910.

—— 1920. Notes on the breeding habits and life-history of the periwinkle. *Fisheries. Ireland. Sci. Inv.* 1920, No. I, pp. 1–11.

THIELE, J., 1929. *Handbuch der systematischer Weichtierkunde*, Teil. 1–2, pp. 1–778.

THORSON, G., 1935. Studies of the egg capsules and development of Arctic marine prosobranchs. *Medd. om Grønland*, Bd. 100, Nr. 5, pp. 1–71.

TRYON, G. W., 1881. *Manual of Conchology*, 310 pp.

VAYSSIÈRE, A., 1923. Recherches zoologiques et anatomiques sur les Mollusques de la famille des Cypraeidés. 1^ère^ Partie. *Ann. Mus. Hist. Nat. Marseille*, Zool., T. XVIII, pp. 1–120.

—— 1930. Étude zoologique et anatomique sur quelques gastéropodes Prosobranches provenant des Campagnes Scientifiques du Prince Albert I^er^ de Monaco. *Rés. Camp. Sci. Albert I^er^*, Fasc. LXXX, 1930, pp. 1–26.

VERRILL, A. E., 1882. Catalogue of Marine Mollusca, added to the Fauna of New England during ten years. Part I. *Trans. Connect. Acad. Sci. and Arts* v, pp. 447–586.

VESTERGAARD, K., 1935. Über den Laich und die Larven von Scalaria communis (Lam.), Nassarius pygmaeus (Lam.) und Bela turricola (Mont.). *Zool. Anz.*, Bd. 109, Heft 7/8, pp. 217–22.

WATSON, R. B., 1885. On the Cerithiopsides from the eastern side of the North Atlantic. *Journ. Linn. Soc.*, Vol. XXIX, pp. 89–95.

WEGMANN, H., 1884. Contribution à l'Histoire Naturelle des Haliotides. *Arch. Zool. Exp. Gén.*, 2^e Sér., II, pp. 289–378.

WILLCOX, M. A., 1905. Biology of *Acmaea testudinalis* Müll. *American Naturalist*, Vol. XXXIX, pp. 325–33.

WILSON, E. B., 1904. Experimental studies in germinal localization. (1) The germ region in the egg of *Dentalium*. (2) Experiments on the cleavage-mosaic in *Patella* and *Dentalium*. *Journ. Exp. Zool.*, Vol. I, pp. 197–268.

WINCKWORTH, R., 1932. The British marine Mollusca. *Journ. Conch.*, Vol. 19, No. 7, pp. 211–52.

—— 1934. Names of British Mollusca. II. *Journn. Conch.*, Vol. 20, No. 1, pp. 9–15.

NOTE. Miss D. R. Crofts' monograph "The Development of *Haliotis tuberculata*, with special reference to Organogenesis during Torsion" (*Phil. Trans. Roy. Soc. London*, Ser. B, Biol. Sci., No. 552, Vol. 228, Oct. 1937) arrived too late to be included in the present work.

OXIDATION-REDUCTION POTENTIAL IN SEA WATER

By L. H. N. Cooper, Ph.D., F.I.C.

Assistant Chemist at the Plymouth Laboratory

In bacteriological studies much attention is now given to oxidation-reduction potentials. The systems studied have usually potentials at least 0·4 V. below that of the reversible oxygen electrode, are reasonably well poised and obey laws thermodynamically deduced. Owing to the irreversibility of the oxygen electrode and to difficulties of measurement no such attention has been given to oxidation-reduction potentials in sea water or other aerated natural waters. Nevertheless, such waters can exert a potential which may be of considerable biological, geological and industrial importance.

One record only of the oxidation-reduction potential of sea water was found in the literature, 0·25 V. recorded incidentally by Reiss & Vellinger (1929) in the course of a study of sea-urchin eggs. Of the 2 mg./l. of organic carbon which Keys, Cristensen & Krogh (1935) have found in sea water, practically nothing is known beyond the fact that it is somewhat inert, how inert we do not know. Since the oxidation-reduction system based on dissolved oxygen appears to be much the most likely to be that giving poise to the water, a theoretical examination of the system was made. Certain thermodynamic properties of sea water, a knowledge of which is required for other investigations, are also treated at some length.

The reaction at an oxygen electrode is:

$$O_2 + 2H_2O + 4\epsilon = 4OH^-.$$

If this reaction can take place reversibly, in the thermodynamic sense, the oxidation-reduction potential of any oxygen electrode, E^h, will be given by

$$E^h = E^\circ - \frac{RT}{4F} \ln \frac{a_{OH^-}{}^4}{a_{O_2}}. \qquad \text{......(1)*}$$

E° is the potential, relative to the normal hydrogen electrode, which should be realized at an inert metal electrode saturated with oxygen at 1 atm. pressure acting in an electrolyte containing hydroxyl-ion at unit activity (nearly equi-

---

* On modern chemical theory a uni-univalent strong electrolyte, dissolved in water, dissociates practically completely into ions each having concentration, m_x. Owing to electrostatic forces between the ions, not all at any instant are able to participate actively in chemical reactions. That part which can do so is termed the activity, a_x, and is related to the concentration by the activity coefficient, γ_x:

$$a_x = \gamma_x m_x.$$

Activity and concentration are measured in the same units. The activity coefficient is a number without dimensions. The activity concept is used wherever it applies so that, for instance, K_w is defined in terms of activities and not, as in most of the earlier work, in terms of concentrations. The system of notation here followed is that of Lewis & Randall (1923).

valent to a normal solution of sodium hydroxide). For reasons which will be made clear below, this standard potential of the oxygen electrode is not realizable in practice.

Equation (1) may be rewritten

$$\mathrm{E^h} = \mathrm{E}^\circ - \frac{\mathrm{RT}}{\mathrm{F}} \ln \frac{a_{\mathrm{OH}^-}}{\sqrt[4]{p_0}}, \qquad \ldots\ldots(2)$$

so that to evaluate $\mathrm{E^h}$ we need to know E°, p_0 and a_{OH^-}. These quantities will be examined in turn.

THE STANDARD OXYGEN ELECTRODE POTENTIAL, E°

At 25° C. E° has been calculated to be 0·3976 V. (Lewis & Randall, 1923, p. 487). For other temperatures E° has been computed from the free energies of formation, and of ionization, of water. We may write three thermodynamic equations, where ΔF°_T represents the increase in free energy of the system concerned with reference to the standard states of the components at the temperature T° abs.:

	ΔF°_T	
H_2O (liquid) $= H^+ + OH^-$	x	......(3)
H_2 (gas) $+ \frac{1}{2}O_2$ (gas) $= H_2O$ (liquid)	y	......(4)
$2H^+ = H_2$ (gas)	0	......(5)

Multiplying (3) by 2, adding (4) and (5) and then dividing by 2 we get

$\frac{1}{4}O_2$ (gas) $+ \frac{1}{2}H_2O$ (liquid) $= OH^-$ ... ... $x+\frac{y}{2}$ ......(6)

From equation (6) E°_T may be calculated by means of (7):

$$\mathrm{E}^\circ_T = -\frac{\Delta F^\circ_T}{\mathrm{F}}. \qquad \ldots\ldots(7)$$

According to *International Critical Tables*, Vol. VII, p. 232, the free energy of ionization, x, at any temperature, T° abs., may be calculated from the relation

$$x = 29210 + 53 \ln T - 335{\cdot}86\,T. \qquad \ldots\ldots(8)$$

Similarly, the free energy of formation

$$y = -70650 - 8{\cdot}0 \ln T + 92{\cdot}84\,T. \qquad \ldots\ldots(9)$$

From these data the free energy changes and electrode potentials relevant to equation (6) have been calculated at temperatures between 0° and 25° C. (Table I). Thus the value of E° decreases linearly by 0·0016 V./degree.

Table I

			Oxygen system, equation (6)	
t° C.	x cal.	$y/2$ cal.	$\Delta F^\circ = x + y/2$ cal.	E°
0	+18684	−28775	−10091	+0·4373
5	+18760	−28676	− 9916	+0·4298
10	+18843	−28576	− 9733	+0·4218
15	+18926	−28476	− 9550	+0·4139
20	+19013	−28379	− 9366	+0·4059
25	+19105	−28280	− 9175	+0·3976

OXYGEN ACTIVITY OR PARTIAL PRESSURE, p_0

Due to the presence of water vapour the partial pressure of oxygen in saturated air varies slightly, but for our present purpose it is sufficient to take a round figure, 0·206 atm., for the partial pressure of oxygen over the sea. The partial pressure of oxygen in sea water at 100 % saturation must be identical with this and measures the oxygen activity. Sea water at various degrees of oxygen saturation will therefore have the following values of p_0 and $\sqrt[4]{p_0}$:

% saturation	p_0	$\sqrt[4]{p_0}$
100	0·206	0·674
50	0·103	0·567
10	0·0206	0·379
1	0·0021	0·213

THE THERMODYNAMIC IONIC PRODUCT, K_w, AND HYDROXYL-ION ACTIVITY, a_{OH^-}

The thermodynamic ionic product, $K_w = \frac{a_{H^+}\, a_{OH^-}}{a_{H_2O}}$, is independent of the presence of solutes, and in consequence in sea water the product of the activities of hydrogen and hydroxyl ions is the same as in pure water except in so far as the presence of salts alters the activity of the undissociated water. However, in moderately concentrated solutions of strong electrolytes, the product of the activity coefficients, $\gamma_{H^+}\,\gamma_{OH^-}$, decreases so that in a solution of sodium chloride, having the same ionic strength as sea water, $\gamma_{H^+}\,\gamma_{OH^-} = 0{\cdot}51$. Therefore

$$m_{H^+}\, m_{OH^-} = \frac{K_w\, a_{H_2O}}{\gamma_{H^+}\,\gamma_{OH^-}} = \frac{K_w\, a_{H_2O}}{0{\cdot}51},$$

that is, if we assume for the moment that the activity of the water a_{H_2O} is unity, the stoichiometric or molal ionic product will be about twice that in pure water. However, pH (so called) determined either electrometrically or with indicators is a measure of activity rather than of concentration of hydrogen ions and is more precisely denoted by pa_H (Sørensen & Linderstrøm-Lang; cf. Clark, 1928, p. 479). Again the majority of physico-chemical computations in aqueous media involve activities of hydrogen and hydroxyl ions and not molal concentrations. Since the uncertainty as to the value of the thermodynamic ionic product, $K_w = \frac{a_{H^+}\, a_{OH^-}}{a_{H_2O}}$, has been removed by the highly accurate and consistent work of Harned and his collaborators, this may be applied as it stands to our sea-water problems.

The activity of the water itself, a_{H_2O}, which has still to be considered, may be evaluated from the depression of the freezing-point of sea water below pure water, $\Delta t°$, by means of the Lewis & Randall equation (1923, p. 284):

$$\log_{10} a_{H_2O} = -0{\cdot}004211\,\Delta t - 0{\cdot}0000022\,\Delta t^2. \qquad \ldots\ldots(10)$$

The necessary freezing-point data were determined by Matthews (1923, p. 667). For a range of chlorinities the values of a_{H_2O} calculated from equation (10), are given in Table II.

Table II. THE ACTIVITY OF WATER, a_{H_2O}, IN SEA WATER

Cl ‰	Δt °C.	a_{H_2O}
0	0·000	1·0000
5	−0·483	0·9953
10	−0·969	0·9906
15	−1·466	0·9858
18	−1·769	0·9830
19	−1·872	0·9820
20	−1·974	0·9810

The product of the ionic activities, $a_{H^+}\,a_{OH^-}$, is equal to K_w only when a_{H_2O} is unity as in pure water. In any aqueous solution the product

$$K'_w = a_{H^+}\,a_{OH^-} = K_w\,a_{H_2O}; \qquad \text{......(11)}$$

$$\therefore\ pK'_w = pK_w - \log_{10} a_{H_2O}. \qquad \text{......(12)}$$

In Table III are given values of pK_w calculated from Harned & Hamer's data (1933) and values of pK'_w for sea water of $35\ ^{\circ}/_{\circ\circ}$ salinity and a range of temperatures calculated from equation (12). It will be seen that the difference between pK_w and pK'_w is of importance only for work of the very highest accuracy. Since from equation (11)

Table III. pK_w FOR PURE WATER AND pK'_w AND SOME VALUES OF pa_{OH} IN SEA WATER OF $35\ ^{\circ}/_{\circ\circ}$ SALINITY AT A RANGE OF TEMPERATURES

		Sea water at $35\ ^{\circ}/_{\circ\circ}$ salinity		
			pa_{OH} at	
t° C.	Pure water pK_w	pK'_w	$pa_H = 8·000$	$pa_H = 8·300$
0	14·939	14·947	6·947	6·647
5	14·731	14·739	6·739	6·439
10	14·533	14·541	6·541	6·241
15	14·345	14·353	6·353	6·053
20	14·167	14·175	6·175	5·875
25	13·997	14·005	6·005	5·705
30	13·832	13·840	5·840	5·540

$$pa_{OH} = pK'_w - pa_H,$$

the value of pa_{OH} for a given sample of sea water can now be found with an accuracy equal to that of the measurement of pa_H, providing that the salinity is known approximately and that the temperature is known to within 0·1° C. Values of pK_w for intermediate temperatures may be found either by graphical interpolation or with great precision from Harned & Hamer's equation (1933):

$$pK_w = \frac{4787·3}{T} + 7·1321 \log_{10} T + 0·010365\ T - 22·801. \qquad \text{......(13)}$$

THE THEORETICAL OXIDATION-REDUCTION POTENTIAL

Using these values for E°, p_0 and a_{OH^-}, the following theoretical values for the oxidation-reduction potential of the oxygen system have been calculated by equation (2) (Table IV):

Table IV. THEORETICAL OXIDATION-REDUCTION POTENTIAL OF THE OXYGEN SYSTEM IN VOLTS

	O_2 = 100 % saturation		O_2 = 10 % saturation	
t° C.	pH 8·00	pH 8·30	pH 8·00	pH 8·30
0	0·804	0·788	0·790	0·774
15	0·767	0·750	0·753	0·735
25	0·742	0·724	0·727	0·710

Thus, decreasing the percentage saturation of oxygen from 100 to 10 % or raising the *p*H by 0·30 unit will each lower the potential by 0·02 V. only. Similarly, raising the temperature by 10° C. will lower the potential by 0·025 V. Thus variations in oxygen concentration, *p*H and temperature within the limits usually found cannot affect the potential by more than about 0·10 V. at most.

We see, therefore, that if the oxidation-reduction potential of sea water is due to a reversible oxygen system, then the potential will lie between 0·7 and 0·8 V. This theoretical discussion has served to clear the ground by giving us values for the reversible potential, E^h, which we can now discuss further in the light of certain peculiar properties possessed by the oxygen electrode.

THE IRREVERSIBLE OXIDATION-REDUCTION POTENTIAL OF SEA WATER

Of prime importance is the practical difficulty involved in measuring the potential at an oxygen electrode. Oxygen electrodes tend to be irreversible, do not obey the thermodynamic relationship between electrode potential and partial pressure of oxygen, and are readily polarized even by minute currents. From a careful examination Hoar (1933) concluded that the platinum used in the electrode forms an oxide film, but that the irreversibility results not so much from the presence of this film but, due to crack formation, to its permeability to the electrolyte which results in self-polarization.

Due to this irreversibility, determinations of the potential by different workers vary considerably. Hoar (1933) has found the potentials of a saturated oxygen electrode against a hydrogen electrode in the same solution, E_β, which should be typical of results obtained with a bright platinum electrode under good working conditions. The difference between the reversible and irreversible potentials of an oxygen electrode will be the same, no matter what half-cell is used as reference electrode so that

Reversible potential against hydrogen in same solution, E_α, *minus* Irreversible potential against hydrogen in same solution, E_β; *equals* Reversible potential against normal hydrogen electrode, E_γ, *minus* Irreversible potential against normal hydrogen electrode, E_δ.

$$\therefore\ E_\delta = E_\gamma - E_\alpha + E_\beta.$$

In Table V Hoar's observed values of E_β are given in column 3 together with the calculated theoretical values of E_γ. Since $E_\alpha = 1{\cdot}2256$ V. (Lewis & Randall, 1923, pp. 408 and 487), E_δ can be readily computed. The *p*H values in *N*/10 H_2SO_4 and *N*/10 NaOH have been calculated from the activity coefficients given by Harned & Hamer (1935) and Harned & Hecker (1933).

Table V

1 Solution	2 *p*H (calc.)	3 Irreversible potential against hydrogen electrode in same solution (Hoar; obs.) E_β	4 Reversible potential against hydrogen electrode in same solution (theoretical) E_γ	5 Irreversible potential against normal hydrogen electrode (calc. from cols. 3 and 4) E_δ
N/10 H_2SO_4	1·47	0·828	1·168	0·770
M/15 phosphate buffer	7·0	0·936	0·813	0·523
N/10 NaOH	12·88	0·981	0·457	0·212

Dr W. R. G. Atkins has very kindly undertaken determinations of the oxidation-reduction potential of sea water, E^h, using bright platinum electrodes which had barely cooled, after having been heated to redness right in a methylated spirit flame. The potentials were measured against a calomel (*N*/10 KCl) half-cell which has a potential against the normal hydrogen electrode of 0·338 V. He found that the potential of sea water lies in the neighbourhood of 0·43 V. Determinations were also made of the E^h and *p*H of sea water acidified with varying amounts of hydrochloric acid. Following the immersion of the electrodes the potential fell away rapidly so that the initial readings were taken as most nearly correct. After the apparatus had been improved enabling several seconds to be saved before making this initial reading, a second series was made which lay somewhat higher than the first. Values of E^h corresponding to the experimental *p*H values have also been read from a curve constructed from Hoar's data (Table V) and are included in Table VI for comparison with Atkins' results which have been rounded off to the nearest centivolt owing to the uncertainty inherent in the measurement. It will be seen that the agreement is considerably better than might have been expected. Furthermore, Heintze (1935) has collected all the evidence available on the E^h of soil solutions and has shown that at *p*H 8·0 most of the values fall between E^h 0·4 and 0·5 V., and that the potential of a standard buffer solution at *p*H 8 lay at about 0·45 V. Thus these measurements also were those of an irreversible oxygen electrode.

It is clear, therefore, that in sea water, the oxidation-reduction potential is governed solely by this irreversible oxygen system. The conclusion is almost certainly of general applicability, so that it should be unnecessary to repeat the

Table VI. OXIDATION-REDUCTION POTENTIAL OF SEA WATER, E^h, IN VOLTS AT A RANGE OF pH VALUES

pH	E^h of oxygen electrode in water at 25° C. (derived from Hoar's results)	E^h of an air electrode in sea water at 15° C.	
		1st series	2nd series
1·09	0·79	0·78	—
2·05	0·75	0·75	0·80
2·14	0·75	0·70	0·76
2·58	0·73	0·69	0·76
3·09	0·71	0·66	0·73
3·55	0·69	0·67	0·72
6·87	0·53	0·57	0·47
7·14	0·52	0·45	0·45
8·15	0·46	0·42	0·44

The potential in water saturated with oxygen at 25° C. should lie close to the potential in water saturated with air at 15° C. If the reversible laws can be applied:

$$E^h\ (\text{air, } 15°\ \text{C.}) = E^h\ (O_2,\ 25°\ \text{C.}) - 0{\cdot}021 + 0{\cdot}002\ p\text{H}.$$

work on sea water from other regions unless there is a strong suspicion that reducing substances able to impart poise to sea water are present.

Although the divergence of the experimental from the theoretical potential is due in the first place to the formation of an oxide film on the electrode, Hoar considers that even with a perfectly inert metal electrode, should such ever be found, the theoretical reversible potential could never be quite reached owing to the extreme sluggishness of the reaction: oxygen $\rightleftharpoons$ hydroxyl-ion. Much more work is required before this point of view, which is not in complete accord with present ideas of ionic reactions, may be taken as established.

Oxidation-reduction potentials lower than that of the irreversible oxygen electrode may well be found off the west African coast in 10° S. latitude, where Wattenberg (1933) found partial pressures of carbon dioxide more than four times that in the atmosphere and where extensive breakdown of organic material is taking place. If the irreversible oxygen potential should be found to prevail in that or similar regions, it may be expected to prevail throughout the open ocean. Since conditions of temperature, partial pressure of carbon dioxide (P_{CO_2}) and pH are as extreme at Meteor Station 188 as at any place that has as yet been fully investigated it is of interest to evaluate the pOH (strictly speaking, pa_{OH}) *in situ* and the reversible oxidation-reduction potential based on the oxygen system (Table VII). In spite of the great depletion of oxygen around 400 m. the temperature remains the dominant factor and the reversible potential increases steadily right through the stratum of stagnant water.

Reactions which depend on the activity of hydroxyl ion *in situ* ($p\text{OH}_t$) will be affected by the change in pK'_w as well as in $p\text{H}_t$. Thus although the values of $p\text{H}_t$ at 25 and 1980 m. are similar the values of $p\text{OH}_t$ differ by 0·75 unit. On account of this, ferric hydroxide, for example, would be more than 200 times as soluble at the greater depth and, in general, solubilities dependent on pOH will be much affected.

Table VII. Station 188 of the Meteor Expedition on September 5 1926 in 8° 58·0′ S., 8° 57·7′ E. (Wattenberg, 1933, pp. 72 and 292). Columns marked with an asterisk contain Wattenberg's data; the remaining columns include data calculated from these

True depth m.*	Temp. °C.*	$P_{CO_2} \times 10^4$*	pH_t†*	$p'K_w$	pOH_t†	O_2 c.c./l.*	E° V.	E^h (reversible) V.
0	22·4	3·2	8·15	14·10	5·95	4·81	0·4017	0·740
25	21·0	3·7	8·09	14·14	6·05	4·52	0·4043	0·746
50	16·2	6·1	7·91	14·31	6·40	1·40	0·4120	0·761
100	14·3	6·9	7·86	14·38	6·52	1·40	0·4148	0·768
195	12·2	8·4	7·78	14·46	6·68	0·88	0·4183	0·775
395	8·5	12·2	7·62	14·60	6·98	0·45	0·4242	0·788
590	5·8	10·7	7·66	14·71	7·05	1·43	0·4285	0·800
785	4·5	8·2	7·76	14·76	7·00	2·72	0·4306	0·801
990	4·1	7·1	7·81	14·78	6·97	3·22	0·4312	0·801
1980	3·3	4·1	8·01	14·81	6·80	5·06	0·4325	0·793

† These quantities would be more strictly written as pa_{H_t} and pa_{OH_t}.

Biological Implications

The implications of the irreversibility of the oxygen electrode system for a study of sea water as a biological environment must now be discussed. Two facts are clear: (i) under no circumstances will the oxygen system function strictly reversibly, but (ii) we are not concerned with a metal electrode which may form porous oxide films. From a system functioning irreversibly less free energy can be got than from the same system functioning reversibly. In consequence the effective oxidation potential will be lower, for this is merely another way of describing the free-energy state of the system, but it does not follow that the biologically effective potential need be as low as that found with a platinum electrode. The effective E^h may vary considerably with the system under investigation according to the greater or less degree of irreversibility of its reaction with oxygen.

The ferric-ferrous system, which is of importance for other investigations in progress here, is recognized as not being very sensitive to oxygen. It has been most studied in the pH range 0–2, where its oxidation-reduction potential is independent of pH and lies only just below that of the irreversible oxygen electrode. The driving force of the reaction of dissolved oxygen with ferrous-ion is therefore small. Moreover, the resulting ferric-ion collects in solution tending to reverse the direction of the reaction. In our problem we are concerned with iron in sea water at pH 8; at this pH the very low solubility of ferric hydroxide results in the removal of ferric-ion from solution as fast as it is formed. In consequence the tendency for ferrous-ion to be oxidized is enormously increased, and solutions of ferrous salts are very unstable and a state approaching equilibrium is rapidly attained. It appears reasonable to extend these conceptions to the very small amounts of iron present in sea water.

This paper has been developed for the particular case of sea water, but the treatment is general and may be extended to all aerated natural waters. In many cases where reducing substances are definitely known not to be present, it may well be sufficiently accurate to read off the irreversible potential from a curve constructed from Hoar's data and to calculate the theoretical reversible potential from equation (2). The potential for biological studies will lie somewhere between these limits; no electrometric measurements can give more information than this. Whilst there must always be some uncertainty in any work involving the oxidation-reduction potential of the oxygen system it is felt that, even so, knowledge of much importance on the behaviour of natural waters may be obtained. In many cases, such as those involving solubilities and the behaviour of multivalent metals, information may be obtained as to what conditions are and what are not possible. Such a case, the behaviour of iron in sea water, will be discussed in a subsequent paper.

SUMMARY

The activity of oxygen in sea water and standard oxygen electrode potentials at a range of temperatures have been computed.

Accurate values for the thermodynamic ionic product of water, K_w, found by Harned & Hamer, have been applied to the calculation of the activity of hydroxyl ion in sea water from *p*H measurements.

The activity of water in sea water has been computed from the lowering of the freezing-point.

From these data the theoretical reversible oxidation-reduction potential of sea water has been calculated.

Typical data for the irreversible potential in the *p*H range 1–8 have been derived from Hoar's results with which experimental determinations made by Dr Atkins agree. Thus the oxidation-reduction potential of sea water is controlled solely by the oxygen system.

The biological implications of the reversible and irreversible (at platinum electrode) potentials is discussed. Under no circumstances will the oxygen system function strictly reversibly, but on the other hand we are not necessarily concerned with metal electrodes which form porous oxide films. It is considered that in sea water the potential effective in systems of biological importance may lie anywhere between 0·43 and 0·75 V., the irreversible (Pt electrode) and reversible potentials.

I am much indebted to Prof. H. T. S. Britton, Exeter, for critical discussion of the subject-matter of this paper and for reading the manuscript. I must, however, be held responsible for the views put forward.

REFERENCES

Clark, W. M., 1928. *The Determination of Hydrogen Ions.* London, 1928. Third edition.

Harned, H. S. & Hamer, W. J., 1933. The ionization constant of water and the dissociation of water in potassium chloride solutions from electromotive forces of cells without liquid junction. *Journ. Amer. Chem. Soc.*, Vol. 55, pp. 2194–206.

—— 1935. The thermodynamics of aqueous sulfuric acid solutions from electromotive force measurements. *Journ. Amer. Chem. Soc.*, Vol. 57, pp. 27–33.

Harned, H. S. & Hecker, J. C., 1933. The thermodynamics of aqueous sodium hydroxide solutions from electromotive force measurements. *Journ. Amer. Chem. Soc.*, Vol. 55, pp. 4838–49.

Heintze, S. G., 1935. Soil oxidation-reduction potentials and *p*H values. *Soil Research* (*Bodenkundliche Forschungen*), Vol. 4, pp. 351–5.

Hoar, T. P., 1933. The mechanism of the oxygen electrode. *Proc. Roy. Soc.* London, A, Vol. 142, pp. 628–46.

Keys, A., Christensen, E. H. & Krogh, A., 1935. The organic metabolism of sea water with special reference to the ultimate food cycle in the sea. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 181–96.

Lewis, G. N. & Randall, M., 1923. *Thermodynamics.* New York and London: McGraw Hill.

Matthews, D. J., 1923. Physical Oceanography. *Dictionary of Applied Physics*, Vol. iii, pp. 665–92. London: Macmillan & Co.

Reiss, P. & Vellinger, E., 1929. Le potentiel d'arrêt des divisions de l'œuf d'Oursin. *Arch. Phys. Biol.*, Vol. 7, pp. 80–101.

Wattenberg, H., 1933. *Wiss. Ergebn. Deutsch. Atlantisch. Exped.* Meteor, 1925–7, Bd. viii.

ON THE RATIO OF NITROGEN TO PHOSPHORUS IN THE SEA

By L. H. N. Cooper, Ph.D., F.I.C.
Assistant Chemist at the Plymouth Laboratory

Harvey (1927) realized that the proportion of nitrate-nitrogen to phosphate-phosphorus is similar both in the depths of the Atlantic and in the water of the English Channel in midwinter. He considered that not only does the decay of plankton organisms give rise to these products in that proportion but also that the requirements of the phytoplankton during life are in the same proportion, since both are almost completely used up by the phytoplankton in the upper layers of the sea during summer. Later Redfield (1934) gathered together data from the Western North Atlantic, the Barents Sea (Kreps & Verjbinskaya, 1932) and the Antarctic (Ruud, 1930), and so was able to show conclusively that the order of the ratio of nitrate-N to phosphate-P is remarkably uniform in the sea and remains so when the store of these salts has been somewhat depleted by plant growth. The ratio lies close to N : P : : 20 : 1 when the salts are expressed as milligram-atoms of the elements concerned or nine times as much nitrate-nitrogen as phosphorus when expressed by weight. Redfield examined the nitrogen and phosphorus content of a number of plankton samples, both plant and animal, and found a mean ratio of 18·2. A number of analyses are also available on samples taken from the English Channel near Plymouth (Table I). The mean ratio is 16·3, similar to Redfield's, and the

Table I. Ratio of Nitrogen to Phosphorus (in gram-atoms) in Plankton Organisms taken in the English Channel at L 4 or two miles east of Eddystone

Date	Sample	mg.-atom N/m.³	N/P
9. iii. 34	Mixed Plankton	0·29	17·2
20. iii. 34	,,	0·32	19·8
26. iii. 34	,,	0·29	16·3
10. v. 34	,,	0·73	17·2
15. v. 34	,,	0·51	16·6
	Diatoms:		
3. iv. 34	Tow-net haul filtered through medium silk, almost entirely diatoms	—	21·6
15. v. 34	Rich in diatoms, particularly *Rhizosolenia*	—	17·0
24. v. 34	*Rhizosolenia*	—	15·5
	Zooplankton:		
5. vi. 36	*Sagitta elegans* mature	—	20·7
5. vi. 36	*Pleurobrachia pileus*	—	12·8
5. vi. 36	Portunid megalopas	—	12·2
5. vi. 36	Portunid zoeas and Crangonid larvae	—	13·7
5. vi. 36	*Callionymus lyra* post larvae	—	11·4

range is from 11·4 to 21·6. Although this ratio of nitrogen to phosphorus varies too much from 20 : 1 for us to speak of it as constant, it is sufficiently remarkable that in the sea as a whole and in plankton organisms, it so seldom shows greater variation.

Considerable deviations in sea water have however been found not only at stations in enclosed seas but also at oceanic stations. These do not necessitate the rejection of the principle but rather do they provide us with a new quantity likely to be of value as an index to the origin of bodies of water and of help in following stages in the nitrogen cycle such as are discussed in the following paper.

In the English Channel at Station E1 in the winter of 1925–26 according to the results of Atkins & Harvey (cf. Cooper, 1933, Table VII) the ratio of nitrate to phosphate (in milligram-atoms) was about nine. By the following year the ratio had risen to thirteen and by 1930–31 to seventeen. At Station L4 only surface and bottom results are available and, since high phosphate figures are often found in the surface layer and do not represent the phosphate content of the water immediately beneath, only a rough estimate of the phosphate content of the whole column can be formed. Bearing this in mind, it is still suggestive that the nitrate-phosphate ratio increased from twelve in the winter 1925–26 to fourteen a year later and further to about twenty-two in 1930–31. Thus we see that change in the nature of the water off Plymouth was attended by an increase in the nitrate-phosphate ratio up to 1930–31. That other changes in the nature of the water have taken place within the last fourteen years is shown by the decrease in the winter phosphate maximum after 1930, the related decrease in young fish and plankton generally and by the displacement of *Sagitta elegans* by *S. setosa* after 1931 (Russell, 1936). It should be pointed out that in this paper phosphate results are all uncorrected for error due to presence of salts or of copper* and have been determined by the Denigès-Atkins method. If the ratio of nitrate to phosphate be assumed ideally to approach a value of twenty when both are expressed in milligram-atoms, then deviations from this ratio must be due to definite causes and must clearly be of interest. It is suggested that the amount by which the ratio found differs from twenty be called "the anomaly of the nitrate-phosphate ratio". To illustrate the anomaly, determinations by Helge Thomsen (1931) on board the *Dana* and by the Discovery Committee's ships (1932) repay examination. Table II shows the ratio for three stations in the *Dana*'s Area I (Straits of Gibraltar and Alboran Sea) and the ratio for the mean nitrate and phosphate values in this area and in six other areas extending the length of the Mediterranean as far as the Aegean Sea. In some cases phosphate was completely absent so that the small amounts of nitrate present yield an infinite

---

* The existence of an error in phosphate determinations in sea water is well established. It does not exceed 25 % but it is still uncertain whether the error is due to the presence of salts, of copper or of both together. Measurements of the error by different workers differ considerably and unpublished work by the writer shows that the issue is far from clear. All data used here are on a comparable basis but are uncorrected.

Table II. NITRATE-PHOSPHATE RATIO (MILLIGRAM-ATOMS)

Station	Position	Date	Depth in metres 50	75	100	150	200	300	400	500	600	800	1000	1200	1500	2000	2500	3000	3500	4000	Mean for all depths
MEDITERRANEAN (*Dana*):																					
4025	Straits of Gibraltar and Alboran Sea	9. iv. 30	27	33	25	38	30	29	35	19	26	32	—	—	—	—	—	—	—	—	30
4027		11. iv. 30	(75)	35	29	32	24	27	47	37	26	25	—	—	—	—	—	—	—	—	31
4140		9. vi. 30	(60)	33	33	28	35	27	—	24	44	—	—	—	—	—	—	—	—	—	32
Area I			(45)	34	29	33	28	28	41	26	32	28	—	—	—	—	—	—	—	—	30
Area II	Balearic Sea, south	11. iv. 30 to 7. vi. 30	(55)	(150)	(106)	(57)	40	41	42	39	34	42	34	40	43	37	50	—	—	—	40
Area III	Sardinia-Tunis	23–25. iv. 30	∞	∞	∞	∞	(350)	(110)	(140)	(96)	—	—	—	—	—	—	—	—	—	—	(high)
Area IV	Tyrrhenian Sea, south	May, 30	0/0	0/0	∞	(93)	25	32	35	31	34	29	23	27	25	28	30	—	30	—	29
Area V	Straits of Messina	5–6. v. 30	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	—	—	—	—	—	—	—	∞
Area VI	Ionian Sea	May, 30	∞	∞	∞	∞	(190)	(125)	(90)	(75)	(64)	54	36	47	42	50	55	43	57	54	49
Area VII	Aegean Sea	17–18. v. 30	0/0	0/0	∞	∞	∞	∞	∞	∞	∞	∞	—	—	—	—	—	—	—	—	∞
ATLANTIC (*Dana*):																					
3978	30° 24′ S, 13° 27′ E	13. ii. 30	8	17	14	18	20	21	19	25	20	19	19	19	22	24	—	—	—	—	19
4000	0° 45′ S, 11° 01′ W	4. iii. 30	9	18	17	15	18	—	20	17	18	19	20	18	15	14	—	—	—	—	16
4009	24° 26′ N, 17° 35′ W	18. iii. 30	0	(3)	(3)	20	16	19	18	18	17	17	17	19	18	16	—	—	—	—	18
4019	33° 08′ N, 10° 22′ W	30. iii. 30	∞	∞	(25)	16	19	20	—	19	24	24	25	24	20	21	20	20	20	20	21
ATLANTIC OFF IBERIAN PENINSULA (*Dana*):																					
4141	36° 11′ N, 6° 57′ W	9. vi. 30	0	0	(20)	24	44	28	27	28	22	27	—	—	—	—	—	—	—	—	29
4142	36° 01′ N, 7° 29′ W	10. vi. 30	0/0	0/0	∞	21	30	28	25	25	33	27	27	—	—	—	—	—	—	—	27
4147	36° 39′ N, 8° 06′ W	10. vi. 30	0	(15)	23	17	23	21	25	25	28	**22**	—	—	—	—	—	—	—	—	23
4148	37° 02′ N, 9° 17′ W	11. vi. 30	∞	(61)	20	25	21	25	27	23	29	**29**	33	28	23	—	—	—	—	—	26
4149	38° 19′ N, 9° 26′ W	11. vi. 30	0/0	∞	(10)	24	27	28	25	25	—	**33**	38	26	25	—	—	—	—	—	28
4156	42° 41′ N, 9° 49′ W	16. vi. 30	∞	∞	33	25	18	25	20	25	23	**28**	23	25	22	25	—	—	—	—	24
BAY OF BISCAY (*Dana*):																					
4158	46° 28′ N, 8° 01′ W	17. vi. 30	12	19	19	17	15	22	19	18	19	21	20	19	16	16	15	15	15	15	17
4159	47° 20′ N, 6° 28′ W	19. vi. 30	(34)	22	19	21	19	18	28	25	25	23	23	—	—	—	—	—	—	—	22
ATLANTIC (Atkins & Harvey, 1925):																					
—	37° 44′ N, 13° 21′ W	12. x. 25	∞	(6)	(35)	(33)	23	19	—	20	—	—	18	—	—	17	—	16	—	—	19

0/0 Both salts had zero concentration.
0 Nitrate zero; phosphate positive.
∞ Nitrate positive; phosphate zero.
( ) Parentheses indicate that either nitrate or phosphate was too low to give a trustworthy ratio.

At 0, 10 and 25 metres at all stations one or both of the salts were absent.

Heavy type denotes water showing a temperature maximum indicating a Mediterranean origin. This water and that immediately above or below shows a high nitrate-phosphate ratio similar to that found inside the Mediterranean.

ratio. Where finite figures emerge, in nearly every case the ratio is much in excess of twenty, implying a large positive anomaly. Thomsen's results showed clearly that the Mediterranean is an impoverished sea, but the present comparison shows further that it is more impoverished in phosphate than in nitrate. In the Straits of Gibraltar the boundary between the incoming surface Atlantic Water and the outgoing deeper Mediterranean water oscillates around 150–200 metres (Murray & Hjort, 1912) so that, judged from the *Dana* stations 4025 and 4140, it appears that both the incoming and outgoing waters in early summer have a large positive anomaly of the nitrate-phosphate ratio. If this state of affairs is usual we have an explanation of the large positive anomaly found in the Mediterranean as a whole.

It is generally recognized that Mediterranean water of high temperature and salinity flows out into the Atlantic around 800 metres and at that depth spreads westwards and northwards. The *Dana* stations 4141 to 4156 lay off the Atlantic Coast of the Iberian peninsula and there Thomsen found temperatures at 800 or 1000 metres higher than in the water above or below. The nitrate-phosphate ratios in these waters of maximum temperature are shown by heavy type in Table II whence it will be seen that these strata or those immediately adjacent have positive anomalies of eight or more; that is, the high anomaly characteristic of Mediterranean water persists after it has flowed out into the Atlantic.

In the Atlantic at Station 661 of *Discovery II* (Table III), at the Discovery Station examined by Atkins & Harvey (1925) and at Stations 3978, 4000, 4009, 4019 and 4158 of the *Dana* (Table II), the ratio conforms closely to

Table III. NITRATE-PHOSPHORUS RATIO IN SOUTH ATLANTIC

(*Discovery II*, 1932)

Station	661		668		673	
Lat.	57° 36′ S		46° 43′ S		38° 37′ S	
Long.	29° 45′ W		30° 22′ W		29° 59′ W	
Date	April 2 1931		April 19 1931		April 24–25 1931	
Depth metres	N/P (mg.-atoms)	Anomaly of N/P ratio	N/P (mg.-atoms)	Anomaly of N/P ratio	N/P (mg.-atoms)	Anomaly of N/P ratio
0	24·5	+4·5	13·4	−6·6	(33·8)	(+13·8)
20	23·2	+3·2	13·4	−6·6	15·2	−4·8
40	23·3	+3·3	13·3	−6·7	17·7	−2·3
60	20·3	+0·3	14·4	−5·6	12·6	−7·4
80	20·0	0·0	13·6	−6·4	17·7	−2·3
100	20·6	+0·6	13·5	−6·5	18·1	−1·9
150	19·0	−1·0	15·4	−4·6	17·0	−3·0
200	18·5	−1·5	17·5	−2·5	22·1	+2·1
400	19·0	−1·0	19·9	−0·1	17·3	−2·7
800	19·1	−0·9	17·6	−2·4	16·8	−3·2
1500	19·0	−1·0	17·0	−3·0	12·4	−7·6
2500	18·4	−1·6	17·2	−2·8	12·6	−7·4
3200	17·6	−2·4	—	—	—	—
3500	—	—	17·3	−2·7	11·5	−8·5
4500	—	—	16·1	−3·9	—	—
Mean	20·2	+0·2	16·6	−3·4	15·9	−4·1

twenty at all depths and the anomaly is small. Other Discovery stations (Tables III and IV) show a large negative anomaly and at Stations 668, 673 and 681 there are obvious variations as different water strata are traversed. An explanation of these results, presumably dependent upon the hydrography of the regions investigated, is beyond the scope of this paper.

Table IV

Discovery II: Station 681; 21° 13′ S, 29° 55½′ W; May 1 1931; mg.-atoms per cubic metre

Depth metres	N	P	N/P	Anomaly of N/P ratio
0–200	0·0–0·5	0·0–0·14	—	—
400	7·15	0·75	9·6	−10·4
800	17·15	1·54	11·2	− 8·8
1500	12·15	1·30	10·7	− 9·3
2500	12·85	1·00	12·9	− 7·1
3500	12·15	0·97	12·5	− 7·5
4900	20·0	1·65	12·1	− 7·9
Mean	—	—	11·5	− 8·5

SUMMARY

Data are presented confirming the belief of Harvey and of Redfield that, in broad outline, the ratio of nitrate-nitrogen and of phosphate-phosphorus in the sea and of nitrogen and phosphorus in marine plankton lies within fairly narrow limits. The ratio approaches twenty to one when expressed in terms of milligram-atoms or nine to one by weight. There are however deviations from this broad generalization, but they do not provide a reason for discarding the concept but rather suggest close examination of the causes of the variations.

The amount by which the N-P ratio in sea water differs from twenty is provisionally termed the "anomaly of the nitrate-phosphate ratio".

It is shown that Mediterranean water possesses a high positive anomaly and that this appears to persist when Mediterranean deep water intrudes into the Atlantic.

The N-P ratio in the English Channel increased between 1926 and 1931.

Attention is drawn to a negative anomaly in certain waters in the South Atlantic.

REFERENCES

Atkins, W, R. G. & Harvey, H. W., 1925. The variation with depth of certain salts utilised in plant growth in the sea. *Nature*, Vol. 116, pp. 784–5.

Cooper, L. H. N., 1933. Chemical constituents of biological importance in the English Channel, November, 1930, to January, 1932. Part I. Phosphate, silicate, nitrate, nitrite, ammonia. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 677–728.

Discovery, 1932. Station List 1929–31. *Discovery Reports*, Vol. iv, pp. 1–232.

Murray, (Sir) John & Hjort, J., 1912. *The Depths of the Ocean*, p. 68. London.

HARVEY, H. W., 1927. *Biological Chemistry and Physics of Sea Water*, p. 48. Cambridge.

KREPS, E. & VERJBINSKAYA, N., 1932. The consumption of nutrient salts in the Barents Sea. *Journ. Cons. Int. Explor. Mer.*, Vol. VII, pp. 25–46.

REDFIELD, A. C., 1934. On the proportion of organic derivatives in sea water and their relation to the composition of plankton. *James Johnstone Memorial Volume*, pp. 176–192. Liverpool.

RUSSELL, F. S., 1936. The importance of certain plankton animals as indicators of water movements in the western end of the English Channel. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. C, pp. 7–10.

RUUD, J. T., 1930. Nitrates and phosphates in the Southern Seas. *Journ. Cons. Int. Explor. Mer*, Vol. V, pp. 347–60.

THOMSEN, H., 1931. Nitrate and phosphate contents of Mediterranean water. *Rep. Dan. Ocean. Exp.*, 1908–10, Vol. 3, No. 6, pp. 1–14.

THE NITROGEN CYCLE IN THE SEA

By L. H. N. Cooper, Ph.D., F.I.C.

Assistant Chemist at the Plymouth Laboratory

(Text-figs. 1 and 2)

Brandt (1899) first suggested that phytoplankton organisms must, by removing from the illuminated surface layers of the sea the nutrients required for their further growth, place a limit on their continued multiplication, and he and Raben for long worked on the problem (see Brandt, 1927, for review of earlier work). The thesis has been proved true beyond all doubt by work which has followed improvements in analytical technique by Atkins and Harvey. In many waters reserves of nitrate are formed during the winter months and are used up, often completely, with the coming of longer days. Interest is now centred on the mechanism by which the nitrate reserve is built up and depleted and on the role played by other compounds of nitrogen. The time has come to review the nitrogen problem as a whole and to assess the importance of many possible reactions in which nitrogen may be involved. The plan of this paper is based on Fig. 1, in which associated reactions are

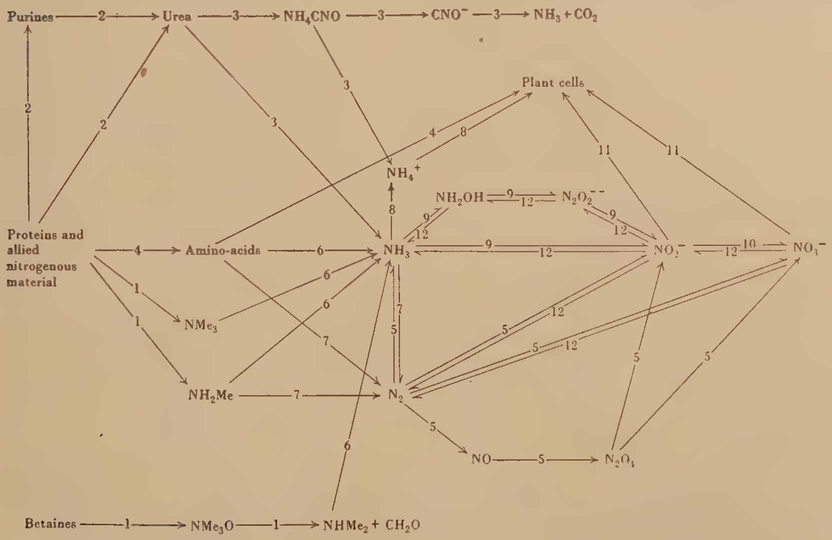

Purines
Urea
NH_4CNO
CNO^-
$NH_3 + CO_2$
Plant cells
NH_4^+
NH_2OH
$N_2O_2^{--}$
Proteins and allied nitrogenous material
Amino-acids
NH_3
NO_2^-
NO_3^-
NMe_3
NH_2Me
N_2
NO
N_2O_4
Betaines
NMe_3O
$NHMe_2 + CH_2O$
1
2
3
4
5
6
7
8
9
10
11
12

Fig. 1. The numbers indicate the reaction group in which the reaction is considered in the text.

numbered in reaction groups. Reactions bearing the same number and the products to which they lead are discussed together.

A complete historical survey would not best serve the purpose of the paper, which is to state the position as seen to-day. Reference to work in the last ten years does not necessarily imply that this was the first in the field in question, but rather that it states the present position and by its aid earlier work may be tracked down. Some reactions are examined from the thermodynamic standpoint, but it must be remembered that thermodynamics is concerned only with initial and final or equilibrium states and, without other help, can give no information as to the rate at which such equilibrium is attained.

NITROGEN IN PARTICULATE MATTER (INCLUDING PLANKTON)

In Atlantic water below 40 m. von Brand (1937) found about 1 mg.-atom nitrogen per cu. m. in particulate matter, including plankton, brought down by a co-precipitation method. In the upper layers where plankton was present in quantity there was two to three times as much. In the Sargasso Sea he found only 0·1 mg.-atom or less.

In 1934 at Station L 4, 8 miles S. 37° W. from this Laboratory, many plankton hauls were taken by Dr Harvey with the quantitative net which has 200 meshes to the linear inch. Analyses were made on some of these by the micro-Kjeldahl method (Cooper, 1934). Between 0·3 and 0·7 mg.-atom N per cu. m. was found (Cooper, 1937*b*, Table I). Since nannoplankton and detritus escaped the net, the concordance with von Brand's results in similar waters is good.

DISSOLVED ORGANIC NITROGEN

Robinson & Wirth (1934 *a*, *b*) have determined albuminoid and organic nitrogen in the waters of the Pacific and of Puget Sound and have summarized earlier investigations. At four deep Pacific stations they found an average of 3 mg.-atom albuminoid-N and 6 mg.-atom organic-N per cu. m. (cf. Brandt, 1927).

REACTION GROUP 1. FORMATION OF METHYLAMINES

In animals considerable quantities of betaines, such as choline, exist and on hydrolysis give rise to trimethylamine oxide. This oxide occurs as such in the muscles of all marine fish yet examined and in many invertebrates, apparently as an end-product of their metabolism; trimethylamine also exists in these fish and in *Fucus vesiculosus* and *F. serratus* (Kapeller-Adler & Krael, 1930 *a*, *b*). The distribution of these compounds in animals has been reviewed by Kutscher & Ackermann (1933, 1936). After death the amine and its oxide are likely to escape into the sea where the oxide may split into dimethylamine and formaldehyde. Mono-, di- and trimethylamine have all been found amongst the excretory products of animals, are generally recognized as breakdown products of proteins, and must be produced in sea water in considerable quantities. When ammonia is determined in sea water by distillation, these methylamines will be included. They will have less effect on Nesslerization methods such as those of Wattenberg and of Buch and Witting (cf. Cooper, 1933*a*, p. 720, Wattenberg, 1937).

Reaction Group 2. Formation of Urea

Purines are commonly formed in the degradation of proteins, and in Lake Mendota in Wisconsin, Peterson, Fred & Domogalla (1925) found 0·7 mg.-atom purine-N per cu. m. By further degradation urea is formed. Large quantities must be liberated into sea water and play there an important although probably transient role. In Lake Mendota, Peterson, Fred & Domogalla (1925) found 0·9 mg.-atom amide-N per cu. m. which may well have been largely urea. Their method of concentration was, however, likely to lead to loss of urea.

Reaction Group 3. Decomposition of Urea

In aqueous solution urea is in equilibrium with ammonium cyanate but in the concentrations usually studied the amount of cyanate is small compared with that of urea. Calculation shows that the conditions in sea water are quite different. The increase in free energy, ΔF°_{298}, in the reaction

$$CO(NH_2)_2 \rightleftharpoons NH_4^+ + CNO^-$$

is +6160 cal. (Lewis & Randall, 1923, p. 587), and from this the equilibrium constant may be computed:

$$\Delta F^{\circ}_{298} = -RT \ln \frac{a_{NH_4^+}\, a_{CNO^-}}{a_{CO(NH_2)_2}} = 6160.$$

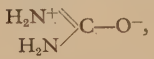
$$\therefore \frac{a_{NH_4^+}\, a_{CNO^-}}{a_{CO(NH_2)_2}} = 3{\cdot}07 \times 10^{-5} \text{ at } 25^{\circ}\text{ C.}$$

∴ in sea water containing 28 mg. NH_4^+-N per cu. m. ($=2\times10^{-6}\,M$), we have

$$a_{CNO^-} = 15{\cdot}35\, a_{CO(NH_2)_2}.$$

At equilibrium, therefore, the activity of the cyanate ion is fifteen times that of the unchanged urea, and with lesser amounts of ammonium ion the equilibrium will still further favour the cyanate ion.

A consideration of the literature on the rate of decomposition of urea (Armstrong & Horton, 1912; Burrows & Fawsitt, 1914; E. A. Werner, 1918; Price, 1919) shows divergence of opinion due to lack of understanding of the structure of urea. To-day urea in solution in water is considered to have the internal salt structure,



where the two amino groups are in resonance and are identical (see Taylor & Baker, 1937, pp. 280–6). The older work needs to be reconsidered with this structure in mind. In the meantime, that the decomposition of urea is unimolecular seems a fair reading. The percentage rate of decomposition at the very great dilutions existing in sea water will be much the same as at higher concentrations and will be assisted by the displacement of the equilibrium discussed above.

The cyanate ion is also hydrolysable by water to ammonia* and carbon dioxide, although little can be surmised as to the state of equilibrium and the reaction kinetics. Even so it is likely that a purely chemical mechanism will suffice to account for the hydrolysis of urea in the sea.

Bacterial hydrolysis with the help of urease is also probable but is considered as augmenting rather than as replacing the chemical hydrolysis above described. Werner (1918) suggests that the mechanism of enzymic hydrolysis by urease is most probably different from the chemical hydrolysis, and his comment that urease is markedly amphoteric fits with the present views on the structure of urea to give the basis of a "lock and key" mechanism. ZoBell & Feltham (1935) claim to have isolated from the sea three different types of urea-splitting bacteria, two of which liberate ammonia.

REACTION GROUP 4. FORMATION AND UTILIZATION OF AMINO-ACIDS

Amino-acids have never been positively identified in sea water but their formation by the degradation of proteins seems more than likely. By concentrating fresh water from Lake Mendota more than 1000-fold Peterson, Fred & Domogalla (1925) determined arginine (3·1 mg.-atom N per cu. m.), tryptophane (0·85 mg.-atom), tyrosine (0·85 mg.-atom), histidine (0·6 mg.-atom) and cystine (0·3 mg.-atom). Similar concentrations are likely to arise in sea water during periods of degradation and to be available to any organisms that can use them.

Since amino-acids are the bricks from which proteins are built, diatoms and other unicellular plants may well use them, when available, as sources of nitrogen. Schreiber (1927) found that there was little to choose between glycine, ammonia, nitrite and nitrate as sources of nitrogen for bacteria-free cultures of *Carteria*. Braarud & Føyn (1930) found that similar cultures of *Chlamydomonas* could use glycine, alanine and asparagine but less efficiently than inorganic nitrogen. Amino-acids must be reckoned as important sources of nitrogen in the sea, but they differ in two respects from available inorganic nitrogen compounds.

Ammonia exists in sea water as the kation NH_4^+ (see p. 189) and nitrite and nitrate as anions, and this ionic character is, no doubt, of importance for their assimilation. By contrast the amino-acids are "zwitterions" or internal salts. Glycine is formulated as $H_3^+N.CH_2.COO^-$, and for the simple amino-acids the amount of zwitterion is 250,000–1,000,000 times that of the uncharged amino-acid (Edsall & Blanchard, 1933). Using the revised values for the dissociation constants of glycine (N. Bjerrum, cited by Taylor & Baker, 1937, p. 108), the ratios of concentrations of the positive ion, $H_3^+N.CH_2.COOH$, m_{A^+}, and of the negative ion, $H_2N.CH_2.COO^-$, m_{A^-}, to the zwitterion, $m_{A^{+-}}$, have been calculated at a number of *p*H values (Table I).

---

* Throughout the paper, "ammonia" is used as an inclusive term for NH_3, NH_4OH, NH_4^+ and ammonium salts in solution.

Table I

*p*H	$\frac{m_{A^+}}{m_{A^{+-}}}$	$\frac{m_{A^-}}{m_{A^{+-}}}$
2	2	$1{\cdot}5\times10^{-8}$
4	2×10^{-2}	$1{\cdot}5\times10^{-6}$
6	2×10^{-4}	$1{\cdot}5\times10^{-4}$
8	2×10^{-6}	$1{\cdot}5\times10^{-2}$
10	2×10^{-8}	$1{\cdot}5$

Thus glycine in sea water will consist of 98·5 % zwitterion and 1·5 % negative ion, with negligible amounts of the positive ion and of the uncharged molecule, $NH_2.CH_2.COOH$. Leucine, α-alanine and β-asparagine will behave similarly to glycine.

Plants require many amino-acids for protein synthesis, and any which are not taken in from the water will have to be freshly synthesized by the plants. Those amino-acids which are taken in by *Chlamydomonas* and *Carteria* in excess of requirements would therefore have to be deaminated within the plant and the resulting ammonia resynthesized into the missing amino-acids.

Reaction Group 5. Fixation of Free Nitrogen

Bacterial fixation of nitrogen has been discussed by Waksman, Hotchkiss & Carey (1933, p. 161). The aerobic *Azotobacter* has been shown to exist in sea water, possibly in symbiosis with marine algae, and anaerobic *Clostridium* in the sea bottom, but their ability to add appreciably to the store of combined nitrogen has yet to be demonstrated.

According to data summarized by F. W. Clarke (1924) the annual deposition of nitric-nitrogen over the sea is likely to be about 2 mg.-atom and of ammonia-N 4–15 mg.-atom per sq. m. In areas of frequent thunderstorms such as the tropics, fixation of nitrogen by electric discharge is likely to be considerably greater. Deacon (1933, p. 219) found 10 mg. nitrate-N per cu. m. in tropical rain water over the sea, and considers this to be the source of the small amount of nitrate found in tropical surface water. Much of the fixed nitrogen found in the sea to-day has no doubt originated by atmospheric fixation, but during a limited period of years the amount so fixed can scarcely affect appreciably the nitrogen balance of the sea as a whole.

REACTION GROUP 6. DEGRADATION REACTIONS PRODUCING AMMONIA

Although deamination of urea is probably a purely chemical reaction, deamination of amino-acids and methylamines in sea water is likely to take place only with the aid of bacteria or enzymes produced by these. The production of ammonia from organic matter in the sea has been shown by Waksman & Carey (1935), von Brand, Rakestraw & Renn (1937) and others. Beesley (1914) studied the rate of nitrification of a number of amino compounds and found that the course of production of ammonia, nitrite and nitrate was essentially the same from urea, uric acid, asparagine, glycine, acetamide, methylamine sulphate, ammonium oxalate and ammonium sulphate. The cultures had been innoculated with bacteria from a sewage filter bed but the results are very similar to those of von Brand, Rakestraw & Renn (1937) who used untreated plankton as source of nitrogen. There was strong evidence of an intermediary between ammonia and nitrite in Beesley's work. There is evidence in favour of this at the end of four weeks in series I of the American team, although the small fall may perhaps not be significant. They consider further that at least part of the amino nitrogen in decaying plankton is liberated directly to the water without first appearing in the form of amino-acids. Beesley's work suggests, however, that the bacterial hydrolysis of amino compounds to ammonia is rapid compared with the prior liberation of amino-acids, so that direct liberation of ammonia is not essential for an explanation of the sea-water results.

In the sea ammonia has been determined at all depths down to 4000 m. but is commonly found in highest concentration at the surface (Böhnecke, Hentschel & Wattenberg, 1930; Cooper, 1933*a*; Robinson & Wirth, 1934*b*).

REACTION GROUP 7. INTERACTION OF METHYLAMINE, AMINO-ACIDS AND AMMONIA WITH NITRITE

Possible loss of nitrogen from methylamine, amino-acids and ammonia by the well-known reaction with nitrite deserves to be considered. The reactions have been examined by Taylor (1928) who found that free nitrous acid is necessary for them to proceed. In each case the underlying mechanism appears to be the same, but for amino-acids, owing to their zwitterion structure, somewhat different velocity equations must be used. Thus for methylamine and ammonia he found

$$-\frac{dm_{\mathrm{R\,.\,NH_3}^+}}{dt}=km_{\mathrm{R\,.\,NH_3}^+}\,m_{\mathrm{NO_2}^-}\,m_{\mathrm{HNO_2}},$$

where R = CH_3 or H, and for glycine and *α*- and *β*-alanine:

$$-\frac{dm_{\mathrm{A}^{+-}}}{dt}=km_{\mathrm{A}^{+-}}\,m_{\mathrm{HNO_2}}^{\;2},$$

where A^{+-} represents the zwitterion form of the amino-acid.

Schümann (1900) determined the ionization constant of nitrous acid, $\frac{m_{H^+} m_{NO_2^-}}{m_{HNO_2}} = 0{\cdot}00045$, whence in sea water containing 0·5 mg.-atom (7 mg.) nitrite-N per cu. m., the concentration of free nitrous acid will be $1{\cdot}1 \times 10^{-5}$ millimol per cu. m. If the water also contains an equal amount of nitrogen as ammonia, methylamine, glycine or α- or β-alanine, the concentration would be reduced by half in a million million years or more. Loss of nitrogen by interaction of amines and nitrite in sea water may therefore be dismissed as of no importance.

Reaction Group 8. Direct Utilization of Ammonia by Plants

Of the ammonia (see footnote, p. 186) determined by distillation and titration a substantial part is likely to be methylamines (p. 185).

The ionization constant of ammonium hydroxide at 18° C.,

$$\frac{a_{NH_4^+} a_{OH^-}}{a_{NH_4OH}} = 17{\cdot}15 \times 10^{-6} \text{ (Noyes \& Kanolt, 1907).}$$

Since at 18° C. when $pH = 8{\cdot}00$, $pOH = 6{\cdot}24$,

$$\therefore\ a_{NH_4^+} = 29{\cdot}8\ a_{NH_4OH}.$$

The term NH_4OH includes anhydrous NH_3, if any. Since the activity of the ammonium ion is only thirty times that of the undissociated base, assimilation of the latter might occur from sea water. However, in terrestrial investigations assimilation of ammonia has been most often observed under acid conditions where the activity of the kation would be many times that of the undissociated base so that in sea water also assimilation of ammonia is most likely in the ionic state.

The availability of ammonia for growth of bacteria-free cultures of *Carteria* and *Chlamydomonas* has been shown by Schreiber (1927) and by Braarud & Føyn (1930) respectively. Schreiber also showed that *Biddulphia mobiliensis* and *Melosira*, and Harvey (1933) that *Nitzschia closterium*, grew on ammonia as well as on nitrate, but these cultures were not bacteria-free. ZoBell (1935*a*) also has shown that *Nitzschia closterium*, *N. bilobata*, *Navicula* sp., *Chlorella* sp. and certain mixed cultures flourished on ammonia nitrogen and, indeed, at the start of his experiments ammonia was even more effective than nitrate. Pearsall & Loose (1937) report a similar result with *Chlorella vulgaris* in fresh water. ZoBell discusses the assimilation of ammonia and there remains no doubt that it provides an excellent source of nitrogen for many marine plants.

It has been claimed that records of ammonia in the sea have failed to show its utilization by diatoms. As against this must be set the small number of results available and the complexity of the changes in which it is continually taking part. On the one hand ammonia in the water is being enriched by degradation processes and on the other it is being removed by oxidation processes and by diatoms. It is not surprising that the picture is less clear than for nitrate. Results at E 1 in the English Channel in mid-April 1931 (Fig. 2) supply unequivocal evidence that, on that occasion at least, ammonia was used during an intensive diatom outburst (Cooper, 1933*a*). Wattenberg & Meyer's results (1936) in Kiel Bay in April 1935 are consonant with this, although other explanations may there be possible. Rakestraw's (1936) results for his station 1739 on the continental shelf off Cape Cod in July give similar evidence.

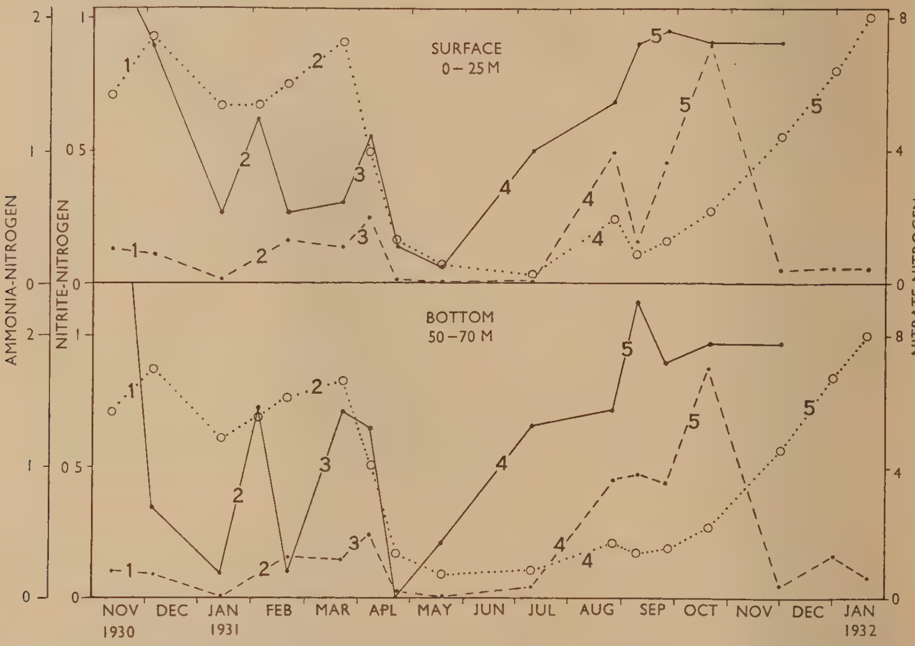


Fig. 2. Ammonia (full line), nitrite (pecked line) and nitrate (dotted line) at Station E 1 in 1930–1, surface and bottom. Stages in the conversion of ammonia to nitrite and thence to nitrate are shown by numbering. In April consumption of all three salts by plankton put a premature end to sequence 3. All as mg.-atom N per cu. m.

Reaction Group 9. Oxidation of Ammonia to Nitrite

The oxidation

$$NH_4^+ + OH^- + \tfrac{3}{2}O_2(\text{gas}) = H^+ + NO_2^- + 2H_2O$$

is accompanied by a decrease in thermodynamic potential or free energy of 59,400 cal. at 25° C. and so requires only to be suitably activated. This activation may be brought about by photochemical, chemical or bacterial agency, and more or less transient intermediates such as hydroxylamine or hyponitrous acid may play a part.

Photochemical Oxidation

Dhar strongly maintains that the oxidation of ammonia in tropical soils is mainly a photochemical process but that certain solid oxides are necessary as photosensitizers (Rao & Dhar, 1931). ZoBell (1933) demonstrated photochemical oxidation of ammonia to nitrite and nitrate by sunlight and by irradiation from a mercury vapour lamp. This result was also achieved by Corbet (1934) who further showed the intermediate formation of hyponitrite. ZoBell found that the reaction went better in natural sea water than in distilled water or artificial sea water. Whether silica exists in sea water in the colloidal or crystalloidal state is yet a matter for debate (Wattenberg, 1937, p. 17) but, since silica was amongst the sensitizers used by Dhar, presence of colloidal particles of silica is a likely explanation of ZoBell's results. He adds that autoclaving sea water at 120° destroyed its photochemical nitrifying power. Since at 120° the ionic dissociation of water is greatly increased, the increased concentration of hydroxyl ion would peptize the colloid, rendering it inactive. Rakestraw & Hollaender (1936) have further confirmed ZoBell's results and found an even greater difference between the behaviour of natural sea water and distilled water.

Photochemical oxidation of ammonia may occur in the surface layers of the sea but, due to the rapid absorption of ultra-violet light in sea water (Atkins & Poole, 1933), will be of no importance below about 1 m.

Chemical Oxidation

On a number of occasions under isothermal conditions we have observed more phosphate and ammonia at the surface than in the water beneath. This has been attributed to the decomposition of organic material floating up to the surface all over the area studied (Atkins, 1930 *b*, p. 829). The decomposition may be assisted by conditions which exist only in the surface layer. Many chemical reactions take place at surfaces and interfaces. Powell & Clarke's contention (1936), that increased light absorption immediately beneath the surface of the sea is due to minute bubbles of air, implies that the greatly increased area of the air-water interface should accelerate the rates of chemical oxidation and hydrolysis.

Bacterial Oxidation

The bacterial oxidation of ammonia to nitrite has been reviewed at length by Barritt (1933). That the oxidation may be brought about either by autotrophic bacteria obtaining their carbon from dissolved carbon dioxide or by heterotrophic bacteria living in symbiosis with diatoms appears in accord with the review and what we know about the sea. However, the work of Kingma Boltjes (1935) which is contrary to this view must be borne in mind. Corbet (1934) believes that in general the autotrophic *Nitrosomonas* is the most important factor in the biological production of nitrite from ammonia, a view which may need modification when applied to the sea and the sea bottom. Kingma Boltjes (1935) has shown that calcium ions, in which the sea is rich, are indispensable for *Nitrosomonas*.

Waksman, Hotchkiss & Carey (1933), Waksman, Reuszer, Carey, Hotchkiss & Renn (1933) and Carey & Waksman (1934) consider their own and earlier results of Thomsen, Issatchenko, Lipman, Harvey and others to be sufficient to show definitely that sea water, especially at the surface, has either no nitrifying bacteria at all or only very few of these organisms. On the other hand, the sea bottom, mud or sand, has an active population of nitrifying organisms to which the formation and accumulation of nitrate in the sea is largely due. From bottom deposits ZoBell (1935*b*) has isolated pure cultures of nitrifiers which oxidize ammonia to nitrite. The oxidation-reduction potentials of such cultures have been determined electrometrically using platinum electrodes. By adjusting the potential with poising substances, the optimum E^h for nitrification was found to be 0·30–0·55 V., multiplication without nitrite formation occurring at somewhat lower potentials. A detailed account of this work is not yet available, but the summarized record is highly suggestive. The optimum E^h is about that of sea water (*ca.* 0·45 V. due to the irreversible oxygen system; Cooper, 1937*a*) and far removed from the low values of E^h which ZoBell & Anderson (1936) have shown often to exist in bottom deposits. The nitrifiers are therefore ideally suited to oxidize ammonia in sea water but not in the deposits from which they were isolated.

There can be no doubt that nitrification immediately above the bottom is of great importance. For example, at the English Channel Station E 1 on August 16 1928, Atkins (1930*a*) found 2·22 mg.-atom nitrite-N per cu. m. immediately above the bottom, and this had increased to 2·67 mg.-atom by August 29. At this time the vertical stability was considerable. Similarly, Cooper (1933*c*) found 1·79 mg.-atom per cu. m. above the bottom at the same station on September 12 1932.

Von Brand, Rakestraw & Renn (1937) have followed the breakdown of plankton *in vitro* and have established clearly the conversion of ammonia to nitrite. Even so, attempts to follow the development of a specific bacterial flora were unsuccessful but opinion in their laboratory appears to consider organisms of the *Nitrosomonas* group to be responsible. Conditions were ideal in their experiments for heterotrophic bacteria perhaps in symbiosis with other organisms. Isolation of the nitrifying bacteria apart from their host would then be difficult.

Thus in the surface layers of the sea oxidation of ammonia to nitrite may be brought about by chemical or photochemical agency, and in and near the sea bottom by bacteria which have been isolated and grown. No one has yet demonstrated any means by which ammonia may be oxidized to nitrite in mid-water but, in spite of this, conversion to nitrite and thence to nitrate does appear to occur in mid-water, and the presence there of nitrite cannot always be accounted for by reduction of nitrate.

In the English Channel on August 16 1932 an intermediate layer of great stability existed (Cooper, 1933*c*), and intense regeneration of silica was there taking place. At the same time a kink in the nitrite vertical profile developed and, although not conclusive, suggests strongly that nitrification was taking place within this layer. A similar conclusion emerges from Atkins' (1930*a*) results in 1928 (Table II). Thus intense nitrification was taking place both at the bottom and in the intermediate layer. There was less activity in between, and the two regions of nitrification appear to have been independent. It is unreasonable to explain the results by oxidation of ammonia in the bottom water and by simultaneous reduction of nitrate in the intermediate layer, more particularly as this same layer of water had almost certainly suffered severe depletion of nitrate during the summer.

Table II. NITRITE AT STATION E 1, AUGUST 1928 (ATKINS). MG.-ATOM N PER CU. M.

Depth m.	August 16 Temp. °C.	August 16 NO_2-N	August 29 Temp. °C.	August 29 NO_2-N
10	15·78	—	15·67	0·00
15	15·67	0·015	15·08	0·31
20	14·92	0·015	13·60	2·78
25	12·70	2·64	13·57	—
40	—	—	12·90	2·06
50	12·65	1·68	12·76	—
65–70*	12·86	2·22	12·74	2·68

* 1–3 m. off bottom.

Similar evidence may be adduced from the survey of the English Channel in 1931 (Cooper, 1933*a* and also Fig. 2) and in Kiel Bight (Wattenberg & Meyer, 1936). At E 1 on a number of occasions formation of ammonia was followed about 3–4 weeks later by an increase in nitrite. In Fig. 2 each event is so numbered that the conversion of ammonia to nitrite and thence to nitrate may be the more readily followed. It may be argued that at a shallow-water station such as E 1, nitrification at the bottom followed by vertical mixing is sufficient to account for the observations. This is sometimes so, but it is very difficult to make the hypothesis fit all the facts. Wattenberg and Meyer's data also show the dependence of nitrite on ammonia but are compatible with the view that nitrification took place at the bottom in 20 m. Soot-Ryen's (1934) work in the neighbourhood of Tromsø gives poor support to the view that nitrification must take place in or near the bottom. Rakestraw (1936, p. 148) points out that at his stations in the Gulf of Maine, nitrite is produced near the surface and works down through the unstable layer during the winter until stratification again sets in.

At all stations investigated by *Discovery II* (1932) in the Southern Ocean, many deeper than 3000 m. (Stations 463, 492 and 646–671 between October and April 1930–1), between 0·3 and 0·7 mg.-atom nitrite-N per cu. m. was found above 150 m. and none below. Many of these stations were sampled in the neighbourhood of 60° S. in early spring or late autumn, so that photochemical oxidation was probably negligible. The results are explainable by reduction of nitrate but, if this is so, certain corollaries follow for which at present there is no other evidence.

In those waters living material is produced in great abundance and in due course dies or is voided to the water as animal faeces. Much of this admittedly sinks into deeper water but some must decompose *in situ* leading eventually to production of ammonia. A small part of this may be photochemically oxidized at the surface but inevitably, failing oxidation, ammonia must accumulate in considerable quantity between, say, 20 and 150 m. The point is capable of experimental test, but at present there is no evidence for such a "hold-up" in the nitrogen cycle in the sea.

Intermediate Formation of Hyponitrite

Beesley (1914) found some evidence for the formation of an intermediary in the bacterial oxidation of ammonia to nitrite, and this has now been identified by Corbet (1935). He pictures the micro-biological oxidation of ammonia as

$$NH_3 \rightarrow NH_2OH \rightarrow H_2N_2O_2 \rightarrow HNO_2 \rightarrow HNO_3,$$

a mechanism in accord with electrochemical views.

At *p*H 6 and over, hydroxylamine has only an ephemeral existence, being destroyed by purely chemical oxidation, and so is unlikely to accumulate in sea water. By contrast calcium hyponitrite is stable in cold aqueous solution and in presence of nitrite. When its aqueous solution was inoculated with soil micro-organisms Corbet found an accumulation of nitrite with no evolution of gas. Conditions in sea water are therefore favourable for the existence of hyponitrite as a stage in the bacterial oxidation of ammonia.

In the autumn of 1931 some experiments were made in this laboratory on the conversion of ammonia to nitrite and nitrate but were then difficult to interpret. They now suggest the intermediate formation of hyponitrite. Water was investigated from two stations, viz. E 1 (5, 50 and 70 m.), as typical of the open English Channel, and L 1 (Plymouth Sound) at high and low water, to give an idea of the behaviour of estuarine water, rich in organic matter and contaminated with sewage.

At Station E 1 the water collected on October 20 1931 was at once run into 300 ml. dark green milk bottles, sterilized at 110° C., in which the experiment was to be carried through. In each bottle an air space of 50 ml. was left. The samples from L 1 were collected in heat-sterilized Winchester bottles on October 23 at low and at high water. Exactly 250 ml. were transferred to sterilized flat-bottomed flasks (500–1000 ml. capacity) for each experiment. Measured quantities of heat-sterilized solutions of ammonia, of nitrite or of both together were added to certain samples in duplicate and some were preserved by mercuric chloride. Analyses for ammonia, nitrite and nitrate were made 8–13 days later (Table III); no nitrate analyses were made on L 1 samples owing to the known presence of much organic matter. The pipettes and measuring cylinders used were chemically clean (cleaning mixture followed by distilled water) but had not been specially sterilized.

Table III. CHANGES IN AMMONIA, NITRITE AND NITRATE + NITRITE IN SEA WATER AND ESTUARINE WATER ON STORAGE

		Initial concentration mg.-atom per cu. m.			Change in x days mg.-atom per cu. m.		
Station, depth and date	$HgCl_2$ present	NH_3-N	NO_2-N	NO_2-N + NO_3-N	NH_3-N per 13 days	NO_2-N per 10 days	NO_2-N + NO_3-N per 13 days
E 1, 5 m., 20. x. 31	−	0·4	0·92	1·9	−0·4	−0·07	−0·2
	−	5·0	0·92	1·9	−1·4	−0·06	Nil
	−	4·9	0·92	1·9	−0·8	−0·08	−0·2
	−	0·4	2·57	3·6	−0·2	−0·07	Nil
	−	0·4	2·76	3·8	−0·2	−0·24	Nil
	−	5·3	2·73	3·7	−1·6	−0·10	Nil
	+	5·2	2·71	3·7	−0·8	−0·05	−0·2
E. 1, 50 m., 20. x. 31	−	0·4	0·89	1·9	−0·1	−0·04	−0·4
	−	4·9	0·89	1·9	−1·3	−0·09	+0·5
	−	5·1	0·89	1·9	−0·6	−0·06	+0·3
	−	0·4	2·71	3·7	−0·4	−0·17	+0·1
	−	0·4	2·47	3·4	−0·4	−0·08	Nil
	−	5·4	2·76	3·7	−1·6	−0·17	−0·1
	+	4·9	2·60	3·6	−0·5	Nil	−0·1
E. 1, 70 m., 20. x. 31	−	0·8	0·86	2·4	−0·6	−0·05	−0·7
	−	5·5	0·86	2·4	−1·7	−0·09	−0·4
	−	5·6	0·86	2·4	−1·4	−0·06	Nil
	−	0·8	2·54	4·1	−0·4	−0·03	−0·8
	−	0·8	2·55	4·1	−0·3	+0·02	−1·0
	−	5·2	2·50	4·1	−1·3	−0·01	−1·1
	+	5·4	2·61	4·0	−0·6	−0·02	−1·0
					per 11 days	per 8 days	
L 1, 0 m., 25 min. before high water, 23. x. 31	−	3·0	0·22	.	+0·3	−0·02	.
	−	8·4	0·22	.	−0·2	−0·03	.
	−	8·4	0·22	.	−1·3	−0·01	.
	−	3·0	1·94	.	+0·1	−0·13	.
	−	3·0	1·94	.	Nil	−0·14	.
	−	8·4	1·94	.	−1·3	−0·14	.
	+	8·4	1·94	.	−1·6	−0·14	.
L 1, 0 m., low water, 23. x. 31	−	6·4	0·32	.	+2·1	+0·04	.
	−	11·0	0·32	.	+0·6	+0·02	.
	−	11·0	0·32	.	+1·4	+0·02	.
	−	6·4	2·04	.	+0·4	−0·15	.
	−	6·4	2·04	.	+0·5	Nil	.
	−	11·0	2·04	.	+0·9	−0·04	.
	+	11·0	2·04	.	−1·0	−0·28	.

In every sample from E 1, ammonia showed a fall. In those samples further enriched with ammonia this fall, amounting to much more than the experimental error, cannot be attributed to nitrite formation. It is highly probable that the ammonia had been oxidized to hyponitrite. Such change in nitrite as occurred was a small loss. In the samples containing mercuric chloride the loss of ammonia is smaller but is still greater than the experimental error. With this account the samples drawn from Plymouth Sound at high water agree. In the low-water samples, the ammonia, already large, increased further in every experiment except that in which mercuric chloride had been added. The bacterial liberation of ammonia in the water rich in organic matter was inhibited. We may conclude that ammonia may be set free from organic matter in sea water by bacterial action and may be converted into a substance such as hyponitrite by a mechanism which need not be bacterial.

Keys, Christensen & Krogh (1935) also found decreases in the ammonia content of sea water on storage but point out that their results are far from consistent. Kreps (1934) has suggested that enzymes, set free from dying bacteria, remain able to oxidize ammonia for a considerable time afterwards even in presence of a bactericide such as mercuric chloride. The stability of nitrite in the L 1 low-water sample subject to heavy contamination from river drainage and urban sewage is worthy of note.

REACTION GROUP 10. OXIDATION OF NITRITE TO NITRATE

The reaction $NO_2^- + \frac{1}{2}O_2(\text{gas}) = NO_3^-$

is accompanied by a decrease of free energy, ΔF°_{298}, of 18,000 cal., so that the reaction requires only activation, and like the oxidation of ammonia it may be used as a direct source of energy by suitably equipped bacteria. Since the equilibrium constant is related to this free energy,

$$\Delta F^\circ_{298} = -RT \ln \frac{a_{NO_3^-}}{a_{NO_2^-}\, a_{O_2}} = -18{,}000 \text{ cal.},$$

therefore with an oxygen activity of 0·2 atmosphere

$$a_{NO_3^-} = 3{\cdot}1 \times 10^{12}\, a_{NO_2^-},$$

and so, in aerated sea water containing 10 mg.-atom (= 140 mg.) nitrate N per cu. m., there will be an equilibrium activity of 3×10^{-12} mg.-atom nitrite N per cu. m., so that at equilibrium nitrite must always be undetectable.

In the building up of nitrate reserves in the sea nitrite is commonly considered an essential intermediary (cf. Atkins, 1930*a*). The investigation in the English Channel in 1931 showed clearly that increase in nitrate followed a few weeks behind the appearance of nitrite (Fig. 2). This result has since been confirmed by the laboratory experiments of von Brand, Rakestraw & Renn (1937) who allowed plankton to decompose in sea water whilst following the conversion of organic nitrogen to ammonia, nitrite and nitrate. Whilst the sea bottom, where nitrite-oxidizing bacteria have been shown to exist by Waksman, Hotchkiss & Carey (1933), is undoubtedly an important site of nitrification, the arguments advanced on pp. 192–4 in favour of oxidation of ammonia to nitrite in mid-water apply equally to the further oxidation of nitrite there.

Reaction Group 11. Assimilation of Nitrite and Nitrate

The ability of phytoplankton to assimilate nitrate needs no discussion. Their power to assimilate nitrite is established on nearly as sound a basis (cf. Schreiber, 1927; Braarud & Føyn, 1930; ZoBell, 1935*a*), but nothing is known as to which would be preferred by a diatom presented with a mixture of salts of ammonium, nitrite and nitrate. At Station E 1 in the English Channel, between April 7 and 22 1931, all three salts decreased together (Fig. 2), strongly suggesting that they were being simultaneously utilized by diatoms. A close relationship between any one of them and diatom growth is hardly to be expected but, since in temperate and arctic latitudes nitrate is the one which collects in sea water during the winter months, it is available in quantity when the spring outburst of diatoms starts. Since Harvey's (1926, 1928) striking investigations in the English Channel, rapid falls in nitrate coincident with this spring outburst have been reported in many waters. At other seasons also, diatom outbursts may lead to depletion of nitrate, but the other nitrogenous compounds are likely then to be available in comparable amounts so that all need to be examined simultaneously if a clear picture of the nitrogen cycle is to be obtained.

Reaction Group 12. Reduction of Nitrate and Nitrite

Since Gran (1901) and Baur (1902) first showed the existence of denitrifying bacteria in the sea, reduction of nitrate and denitrification generally have been a fruitful source of controversy. The view long maintained by Brandt (1927), that true denitrification leading to loss of free nitrogen is of great importance in the sea, finds little support to-day (cf. Atkins, 1932). The literature has been reviewed by Lloyd (1931 *a*, *b*, *c*) and by Waksman, Hotchkiss & Carey (1933). The work of the Wood's Hole Oceanographical Laboratory has shown that the activities of most of the nitrate-reducing bacteria are limited to the reduction of nitrate to nitrite, a reaction leading to no loss of available nitrogen.

Gran (1901) considered that denitrifying organisms do not use nitrate if oxygen is available but observations by other workers suggest that this is not always so. Braarud & Klem (1931) found rapid depletion of nitrate in aerated sea water and Kreps (1934) has described a number of experiments to like effect. The fall in nitrate occurred whether or not mercuric chloride had been added. The writer in his 1931 experiments (Table III) also observed that depletion of nitrate occurred in bottom water from Station E 1 both in absence and presence of mercuric chloride. Kreps also found that the depletion of nitrate could go on in water which had been filtered through a Seitz filter and concluded that enzymes liberated by bacteria into the water were responsible for nitrate reduction and ammonia oxidation, and that these enzymes could pass a Seitz filter and withstand a bactericide such as mercuric chloride.

Waksman, Hotchkiss & Carey (1933) and Waksman, Reuszer, Carey, Hotchkiss & Renn (1933) say little of the effect of oxygen but aerated conditions are implicit in the description of their experiments demonstrating the existence in the sea of bacteria able to reduce nitrate to nitrite. Such bacteria may on occasion account for nitrite found between 25 and 150 m. (Rakestraw, 1933).

This reduction is accompanied by oxidation of organic matter, and the view has been expressed to the writer that it is a wasteful method for a bacterium to obtain energy from nitrate when oxygen is available. If dextrose be considered as source of carbon the changes in free energy or thermodynamic potential, ΔF°, are readily calculated, thus for 25° C.:

$$C_6H_{12}O_6(\text{aq.}) + 12NO_3^- = 12NO_2^- + 6CO_2(\text{aq.}) + 6H_2O(\text{liq.}); \quad \Delta F^\circ = -460 \text{ kg.-cal.}$$

$$C_6H_{12}O_6(\text{aq.}) + 8NO_2^- = 4N_2(\text{aq.}) + 4CO_3^{=} + 2CO_2(\text{aq.}) + 6H_2O(\text{liq.}); \quad \Delta F^\circ = -728 \text{ kg.-cal.}$$

$$C_6H_{12}O_6(\text{aq.}) + 6O_2(\text{aq.}) = 6CO_2(\text{aq.}) + 6H_2O(\text{liq.}); \quad \Delta F^\circ = -699 \text{ kg.-cal.}$$

The thermodynamic efficiencies of the oxidation of a sugar by oxygen and by nitrite are similar. With nitrate, itself simultaneously reduced to nitrite, the efficiency of the oxidation is reduced by one-third. Even so, bacterial reduction of nitrate in aerated water containing oxidizable organic matter cannot be dismissed as an excessively wasteful process. To assimilate the nitrate or nitrite, osmotic work must be done, but this amounts to not more than 1 or 2 kg.-cal. per g.-mol. of dextrose oxidized. If any other carbohydrate, fat or protein were taken a similar result would emerge. No account is taken of the mechanism of the oxidation. Both the straightforward oxidation of nitrite to nitrate and the respiratory reduction of nitrate to nitrite in presence of an organic substance are processes from which energy may be derived.

Korsakov (1929) has regarded the nitrate-nitrite system from the point of view of oxidation-reduction potential. The reduction can take place only if the compounds in the medium can be activated by the bacteria in such a way that one becomes the acceptor and one the donator of hydrogen. Aerobic bacteria are able to activate not only the system, donator of hydrogen (organic substance) + acceptor (oxygen), but also systems involving other acceptors (e.g. nitrate ion). Owing to the thermodynamic irreversibility of the nitrate-nitrite system arguments such as this are somewhat dangerous but, if the reduction of nitrate is regarded as dependent on oxidation-reduction potential, sea water provides a very uniform medium. There is evidence arising out of work on the iron system in this laboratory that diatoms possess a skin or shell where the potential is much lower than in the water. In this, extracellular reduction of nitrate might take place in the way visualized by ZoBell (1935 *a*). Under some circumstances part of this nitrite may escape assimilation and be returned to the water. Production of nitrite in nitrate-enriched diatom cultures has often been observed (Orr, 1926; ZoBell, 1935 *a*), whilst Warburg & Negelein (1920) found that nitrate was reduced to ammonia by *Chlorella* in pure culture with great rapidity, a fact repeatedly confirmed by Pearsall & Loose (1937).

Photochemical reduction of nitrate to nitrite has been suggested (Moore, 1919) but Villars (1927) showed that the quantum yield at *p*H 8·0–8·3 for wave-lengths greater than 2800 A. was very low. Since only light longer than 2900 A. reaches the earth (Pettit, 1932) and at 3030 A. is cut down to 0·01 % in the first 2·4 m. of sea water (Atkins & Poole, 1933), photochemical reduction of nitrate cannot occur in the sea.

Hyponitrites also occur as intermediates in the reduction of nitrite to nitrogen (Blom, 1928 *b*; Lloyd & Cranston, 1930). Owing to the absence of data for hyponitrite the free-energy change of the reaction cannot be calculated. The heat set free by the reaction

$$C_6H_{12}O_6(\text{aq.}) + 12NO_2^- = 6N_2O_2^{=} + 6CO_2(\text{aq.}) + 6H_2O(\text{liq.})$$

is 376 kg.-cal., and the decrease in free energy is unlikely to differ greatly from this. Reduction of nitrate in the sea may well go as far as hyponitrite.

The evidence is therefore strong that reduction of nitrate in aerated sea water is readily brought about under laboratory conditions, and such reduction should sometimes occur. But as yet, in mid-water, we are not justified in attributing all nitrite formation to reduction of nitrate and dismissing oxidation of ammonia as of no account.

DISCUSSION

Our clear-cut picture of the annual cycle of nitrate in the sea has been obtained because, during the winter in temperate and arctic latitudes, nitrate is accumulated in quantity greater than other available forms of nitrogen. It is therefore ready to be consumed in quantity during the vernal diatom outburst when its variations may be followed by analysis. It is also clear why nitrate formation, requiring a number of successive stages, lags behind phosphate formation.

Since growing plants are well able to use other forms of nitrogen when these are present, analyses of nitrate alone are less likely to give an intelligible picture of events in summer and autumn. The analytical methods for nitrate determine nitrite as well, but when considerable quantities of nitrite are present, results will usually be somewhat too low but, even so, are usually a sufficient measure of nitrate + nitrite.

Our present knowledge of hyponitrite rests on soil and sewage cultures. Its probable existence in the sea requires study for an understanding of the transformations of inorganic nitrogen compounds. Ammonia is certainly of great value, but its determination still presents analytical difficulties (cf. Wattenberg, 1937). In addition, the results may be uncertain due to the presence of methylamines whose value as immediate sources of nitrogen for phytoplankton is unknown.

We can only speculate as to the existence and behaviour of amino-acids and urea in sea water. Amino-acids are known to be of value to certain marine plants, but their assimilation, due to their "zwitterion" structure, may follow a different mechanism from the inorganic ions. They are probably of value only as accessory nutrients. Analytical methods for amino-acids in sea water have still to be developed. The presence of urea in sea water is probably transient but important in the degradation of nitrogen.

It is clear that no one explanation will cover all the oxidation and reduction reactions in which ammonia, nitrite, nitrate and possibly hyponitrite take part. The oxidation of ammonia to nitrite and thence to nitrate may take place photochemically or chemically in a thin surface layer or bacterially in and near the bottom. No bacteria able to bring about the oxidation of ammonia or nitrite have yet been found in sea water well away from the bottom, and the view is maintained by some investigators that no such oxidation can take place there. Bacterial reduction of nitrate to nitrite undoubtedly can and does occur in the sea. In spite of this the writer feels that reduction of nitrate fails to explain all cases of nitrite occurrence in mid-water, that there is strong chemical evidence that oxidation of ammonia does take place away from the bottom and from the immediate surface layer, and that any theory which fails to take these into account cannot cover all the observations.

SUMMARY

The nitrogen cycle in the sea is reviewed as a whole in accordance with the scheme set out in Fig. 1. This summary includes only original matter, since the survey of other work does not admit of further condensation.

The metabolism has been discussed of the following sources of nitrogen available to plants in sea water: mono-, di- and trimethylamine, trimethylamine oxide, urea, amino-acids, ammonia, hyponitrite, nitrite and nitrate. The methylamines will interfere in analyses of ammonia by distillation.

Thermodynamic methods have been extensively used. The equilibrium between urea and ammonium cyanate at sea-water concentrations favours the cyanate. In sea water containing 28 mg. ammonia N per cu. m., the equilibrium mixture will contain fifteen times as much cyanate as urea. Hydrolysis of urea is probably purely chemical.

The importance of the "zwitterion" or internal salt structure of amino-acids in studies on their assimilation is examined. In sea water, the common amino-acids will consist of about 98·5% zwitterion, $H_3{}^+N.R.COO^-$, and

1·5 % anion, $H_2N.R.COO^-$, with negligible amounts of kation and uncharged molecule, $H_2N.R.COOH$. If ever an amino-acid should form the sole source of nitrogen for diatoms, at least part must be deaminated within the plant before other necessary amino-acids can be synthesized.

It is shown from kinetic measurements that no loss of amino-nitrogen can occur by interaction with nitrite in sea water. The activity of NH_4^+ in sea water is about thirty times that of NH_4OH. The change in thermodynamic potential or free energy during the oxidation of 1 g.-mol. of ammonia to nitrite or of nitrite to nitrate is 59·4 or 18 kg.-cal. respectively.

The greater efficiency of photochemical oxidation of ammonia in sea water than in distilled water may be due to the presence of colloidal silica but such oxidation is of no importance below about 1 m. Purely chemical oxidation at the interface with minute air bubbles may be possible immediately beneath the surface of the sea.

Although bacteria able to oxidize ammonia and nitrite have been satisfactorily demonstrated only in bottom water, strong evidence is presented that similar oxidations must proceed away from the sea bottom, by mechanisms yet to be established.

Evidence is marshalled in favour of the intermediate formation of hyponitrite during the oxidation of ammonia to nitrite.

At thermodynamic equilibrium, the activity of nitrate will be 10^{12} times that of nitrite.

Oxidation of 1 g.-mol. of dextrose by nitrate ion, nitrite ion and dissolved oxygen is accompanied by a free energy decrease of 460, 730 and 700 kg.-cal. respectively. Denitrification in aerated water is therefore not excluded on thermodynamic grounds. Even so, reduction of nitrate cannot explain all cases of nitrite occurrence in mid-water. Photochemical reduction of nitrate cannot occur in the sea.

REFERENCES

Armstrong, H. E. & Horton, E., 1912. Studies on enzyme action. XV. Urease: a selective enzyme. *Proc. Roy. Soc.*, Ser. B, Vol. 85, pp. 109–27.

Atkins, W. R. G., 1930*a*. Seasonal changes in the nitrite content of sea water. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 515–18.

— 1930*b*. Seasonal variations in the phosphate and silicate content of sea water in relation to the phytoplankton crop. Part V. November 1927 to April 1929, compared with earlier years from 1923. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 821–52.

— 1932. Nitrate in sea-water and its estimation by means of diphenylbenzidine. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 167–92.

Atkins, W. R. G. & Poole, H. H., 1933. The photoelectric measurement of the penetration of light of various wave-lengths into the sea and the physiological bearing of the results. *Phil. Trans. Roy. Soc.*, Ser. B, Vol. 222, pp. 129–64.

Barritt, N. W., 1933. The nitrification process in soils and biological filters. *Ann. Appl. Biol.*, Vol. xx, pp. 165–84.

Baur, E., 1902. Ueber zwei denitrificirende Bakterien aus der Ostsee. *Wiss. Meeresuntersuch., Abt. Kiel*, N.F., Bd. vi, pp. 9–22.

BEESLEY, R. M., 1914. Experiments on the rate of nitrification. *Journ. Chem. Soc.*, Vol. cv, pp. 1014–24.

BLOM, J., 1928*a*. Zum Nachweis von Hydroxylamin. *Biochem. Zeits.*, Bd. 194, pp. 385–91.

— 1928*b*. Bildung von Hydroxylamin bei der Reduktion von Nitraten durch Mikroorganismen. *Biochem. Zeits.*, Bd. 194, pp. 392–409.

BÖHNECKE, G., HENTSCHEL, E. & WATTENBERG, H., 1930. Über die hydrographischen, chemischen und biologischen Verhältnisse an der Meeresoberfläche zwischen Island und Grönland. *Ann. d. Hydr.*, Jahrg. 58, pp. 233–50.

BRAARUD, T. & FØYN, B., 1930. Beiträge zur Kenntnis des Stoffwechsels im Meer. *Avh. Norske Videnskap Akad.*, No. 14, pp. 1–24.

BRAARUD, T. & KLEM, A., 1931. Hydrographical and chemical investigations in the coastal waters off Møre and in the Romsdalsfjord. *Hvalrådets Skr.*, No. 1, p. 58.

BRAND, T. VON, 1937. Observations upon the nitrogen of the particulate matter in the sea. *Biol. Bull.*, Vol. LXXII, pp. 1–6.

BRAND, T. VON, RAKESTRAW, N. W. & RENN, C. E., 1937. The experimental decomposition and regeneration of nitrogenous organic matter in sea water. *Biol. Bull.*, Vol. LXXII, pp. 165–75.

BRANDT, K., 1899. Ueber den Stoffwechsel im Meere. *Wiss. Meeresuntersuch., Abt. Kiel*, N.F., Bd. IV, pp. 213–30.

— 1927. Stickstoffverbindungen im Meere. I. *Wiss. Meeresuntersuch., Abt. Kiel*, N.F., Bd. XX, pp. 201–92.

BURROWS, G. J. & FAWSITT, C. E., 1914. The decomposition of carbamide. *Journ. Chem. Soc.*, Vol. CV, pp. 609–23.

CAREY, C. L. & WAKSMAN, S. A., 1934. The presence of nitrifying bacteria in deep seas. *Science*, Vol. 79, pp. 349–50.

CLARKE, F. W., 1924. The data of geochemistry, 5th edn., *U.S. Geol. Survey Bull.* 770, p. 55.

COOPER, L. H. N., 1933 *a* and *b*. Chemical constituents of biological importance in the English Channel, November, 1930, to January, 1932. Part I. Phosphate, silicate, nitrate, nitrite, ammonia. Part II. Hydrogen ion concentration, excess base, carbon dioxide, and oxygen. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 677–728 and 729–54.

— 1933*c*. Chemical constituents of biological importance in the English Channel. Part III. June-December, 1932. Phosphate, silicate, nitrite, hydrogen ion concentration, with a comparison with wind records. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 55–62.

— 1934. The determination of phosphorus and nitrogen in plankton. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 755–60.

— 1937*a*. Oxidation-reduction potential in sea water. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 167–76.

— 1937*b*. On the ratio of nitrogen to phosphorus in the sea. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 177–82.

CORBET, A. S., 1934 and 1935. The formation of hyponitrous acid as an intermediate compound in the biological or photochemical oxidation of ammonia to nitrous acid. I. Chemical reactions. II. Microbiological oxidation. *Biochem. Journ.*, Vol. XXVIII, pp. 1575–82; Vol. XXIX, pp. 1086–96.

DEACON, G. E. R., 1933. A general account of the hydrology of the Southern Ocean. *Discovery Reports*, Vol. VII, pp. 171–238.

DISCOVERY INVESTIGATIONS, 1932. Station list, 1929–31. *Discovery Reports*, Vol. IV, pp. 1–232.

EDSALL, J. T. & BLANCHARD, M. H., 1933. Activity ratio of zwitterions and uncharged molecules in ampholyte solutions. Dissociation constants of amino acid esters. *Journ. Amer. Chem. Soc.*, Vol. 55, pp. 2337–53.

GRAN, H. H., 1901. Studien über Meeresbakterien. I. Reduction von Nitraten und Nitriten. *Bergens Mus. Aarbog*, No. 10, pp. 1–23.

HARVEY, H. W., 1926 and 1928. Nitrate in the sea. I and II. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 71–88 and Vol. XV, pp. 183–90.

— 1933. On the rate of diatom growth. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 253–76.

KAPELLER-ADLER, R. & KRAEL, J., 1930*a*. Untersuchungen über die Stickstoffverteilung in den Muskeln verschiedener Tierklassen. II. Über die Stickstoffverteilung im Rochen- und Haifischmuskel. *Biochem. Zeits.*, Vol. 224, pp. 364–77.

— — 1930*b*. Über das Auftreten von methylierten Stickstoffverbindungen im Seetang. *Biochem. Zeits.*, Vol. 224, pp. 378–83.

KEYS, A., CHRISTENSEN, E. H. & KROGH, A., 1935. The organic metabolism of sea water with special reference to the ultimate food cycle in the sea. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 181–96.

KINGMA BOLTJES, T. Y., 1935. *Arch. Mikrobiol.*, Vol. 6, p. 79; *Ann. Rev. Biochem.*, 1936, Vol. V, p. 539.

KORSAKOV, M. P., 1929. (Reduction of nitrates by bacteria.) *Russ. Microbiol. Journ.*, Vol. 9, p. 108; *Brit. Chem. Abst.*, A, pp. 265–6 (1931).

KREPS, E., 1934. Organic catalysts or enzymes in sea water. *James Johnstone Memorial Volume*, Liverpool, pp. 193–202.

KUTSCHER, F. & ACKERMANN, D., 1933, 1936. The comparative biochemistry of vertebrates and invertebrates. *Ann. Rev. Biochem.*, Vol. II, pp. 355–76; Vol. V, pp. 452–62.

LEWIS, G. N. & RANDALL, M., 1923. *Thermodynamics*. New York: McGraw Hill.

LLOYD, B., 1931*a*. A marine denitrifying organism. *Journ. Bact.*, Vol. 21, pp. 89–96.

— 1931*b*. Bacterial denitrification: an historical and critical survey. *Journ. Roy. Tech. Coll. Glasgow*, pp. 530–50.

— 1931*c*. Muds of the Clyde Sea area. II. Bacterial content. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 751–65.

LLOYD, B. & CRANSTON, J. A., 1930. Studies in gas production by bacteria. *Biochem. Journ.*, Vol. XXIV, pp. 529–48.

MOORE, B., 1919. Formation of nitrites from nitrates in aqueous solution by the action of sunlight. *Proc. Roy. Soc.* B, Vol. 90, pp. 158–67.

NOYES, A. A. & KANOLT, C. W., 1907. The electrical conductivity of aqueous solutions. *Publ. Carnegie Inst.*, No. 63, p. 290.

ORR, A. P., 1926. The nitrite content of sea water. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 55–61.

PEARSALL, W. H. & LOOSE, L., 1937. The growth of *Chlorella vulgaris* in pure culture. *Proc. Roy. Soc.*, B, Vol. 121, pp. 451–501.

PETERSON, W. H., FRED, E. B. & DOMOGALLA, B. P., 1925. The occurrence of amino acids and other organic nitrogen compounds in lake water. *Journ. Biol. Chem.*, Vol. 63, pp. 287–95.

PETTIT, E., 1932. Measurements of ultra-violet solar radiation. *Astrophys. Journ.*, Vol. 75, pp. 185–221.

POWELL, W. M. & CLARKE, G. L., 1936. The reflection and absorption of daylight at the surface of the ocean. *Journ. Opt. Soc. Amer.*, Vol. 26, pp. 1–23.

PRICE, T. W., 1919. The decomposition of carbamide in the presence of nitric acid. *Journ. Chem. Soc.*, Vol. XCV, pp. 1354–60.

RAKESTRAW, N. W., 1933. Studies in the biology and chemistry of the Gulf of Maine. I. Chemistry in the waters of the Gulf of Maine in August 1932. *Biol. Bull.*, Vol. LXIV, pp. 149–58.

— 1936. The occurrence and significance of nitrite in the sea. *Biol. Bull.*, Vol. LXXI, pp. 133–67.

RAKESTRAW, N. W. & HOLLAENDER, A., 1936. Photochemical oxidation of ammonia in sea water. *Science*, Vol. 84, pp. 442–3.

Rao, G. G. & Dhar, N. R., 1931. Photosensitized oxidation of ammonia and ammonium salts and the problem of nitrification in soils. *Soil Science*, Vol. 31, pp. 379–84.

Robinson, R. J. & Wirth, H. E., 1934*a*. Report on the free ammonia, albuminoid nitrogen and organic nitrogen in the waters of the Puget Sound area, during the summers of 1931 and 1932. *Journ. Cons. Int. Explor. Mer*, Vol. IX, pp. 15–27.

— — 1934*b*. Free ammonia, albuminoid nitrogen, and organic nitrogen in the waters of the Pacific Ocean off the coasts of Washington and Vancouver Island. *Journ. Cons. Int. Explor. Mer*, Vol. IX, pp. 187–95.

Schreiber, E., 1927. Die Reinkultur von marinem Phytoplankton und deren Bedeutung für die Erforschung der Produktionsfähigkeit des Meerwassers. *Wiss. Meeresuntersuch., Abt. Helgoland*, N.F., Bd. XVI, No. 10, pp. 1–34.

Schümann, 1900. *Ber. deut. chem. Ges.*, Vol. 33, p. 527; *cit.* Lewis & Randall, 1923.

Soot-Ryen, T., 1934. Hydrographical investigations in the Tromsø district 1930. *Tromsø Museums Årshefter*, Vol. 52, pp. 1–78+i–xxx.

Taylor, T. W. J., 1928. The action of nitrous acid on amino-compounds. Part I. Methylamine and ammonia. Part II. Aliphatic amino-acids. *Journ. Chem. Soc.*, pp. 1099–1105; 1897–1906.

Taylor, T. W. J. & Baker, W., 1937. Revised edition of N. V. Sidgwick's *Organic Chemistry of Nitrogen*. Oxford.

Villars, D. S., 1927. The photolysis of potassium nitrate. *Journ. Amer. Chem. Soc.*, Vol. 49, pp. 326–37.

Waksman, S. A. & Carey, C. L., 1935. Decomposition of organic matter in sea water by bacteria. II. Influence of addition of organic substances upon bacterial activities. *Journ. Bact.*, Vol. 29, pp. 545–61.

Waksman, S. A., Hotchkiss, M. & Carey, C. L., 1933. Marine bacteria and their role in the cycle of life in the sea. II. Bacteria concerned in the cycle of nitrogen in the sea. *Biol. Bull.*, Vol. LXV, pp. 137–67.

Waksman, S. A., Reuszer, H. W., Carey, C. L., Hotchkiss, M. & Renn, C. E., 1933. Studies on the biology and chemistry of the Gulf of Maine. III. Bacteriological investigations of the sea water and marine bottoms. *Biol. Bull.*, Vol. LXIV, pp. 183–205.

Warburg, O. & Negelein, E., 1920. (The reduction of nitric acid by green cells.) *Biochem. Zeits.*, Vol. 110, pp. 66–115; *Chem. Abst.*, Vol. 15, p. 380 (1921).

Wattenberg, H., 1937. Critical review of the methods used for determining nutrient salts and related constituents of sea water. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. CIII, pp. 1–33.

Wattenberg, H. & Meyer, H., 1936. Der jahreszeitliche Gang des Gehalts des Meerwassers an Planktonnährstoffen in der Kielen Bucht im Jahre 1935. *Kieler Meeresforschungen*, Bd. 1, pp. 264–78.

Werner, E. A., 1918. The constitution of carbamides. Part V. The mechanism of the decomposition of urea when heated in solution with alkalis and with acids respectively. The hydrolysis of metallic cyanates. *Journ. Chem. Soc.*, Vol. CXIII, pp. 84–99.

ZoBell, C. E., 1933. Photochemical nitrification in sea water. *Science*, Vol. 77, pp. 27–8.

— 1935*a*. The assimilation of ammonium nitrogen by *Nitzschia closterium* and other marine phytoplankton. *Proc. Nat. Acad. Sci.*, Vol. 21, pp. 517–22.

— 1935*b*. Oxidation-reduction potentials and the activity of marine nitrifiers. *Journ. Bact.*, Vol. 29, p. 78.

ZoBell, C. E. & Anderson, D. Q., 1936. Vertical distribution of bacteria in marine sediments. *Bull. Amer. Assoc. Petroleum Geologists*, Vol. 20, pp. 260–9.

ZoBell, C. E. & Feltham, C. B., 1935. The occurrence and activity of urea-splitting bacteria in the sea. *Science*, Vol. 81, pp. 234–6.

THE SUPPLY OF IRON TO DIATOMS

By H. W. Harvey, Sc.D., M.A.
Hydrographer at the Plymouth Laboratory

(Text-figs. 1–2)

INTRODUCTION

Several factors which influence, and from time to time control, the production of phytoplankton can now be enumerated with some degree of certainty—the concentration of phosphate and of nitrate, the illumination and temperature, the rate at which the organisms are being eaten by zooplankton, and the extent to which vertical currents carry them down beyond the level of sufficient light. Instances are indeed known where one or other of these factors has played a preponderating part in regulating the plant life in the sea.

Based on growth in culture solution, Gran (1931, p. 41) concluded that lack or low concentration of iron probably limited plant growth at times and in areas of the sea where it was not replenished by land drainage. Previous data, and those obtained by Braarud & Klem (1931) off the Norwegian coast at his instigation, showed the iron content of sea water to be very small, ranging from 3 to 21 mg. Fe per $m.^3$ Seiwell (1935), by a method which would detect 1–2 mg. per $m.^3$, found the upper forty metre layer at one position in the Atlantic devoid of iron. Cooper (1935) obtained similar values to those of Braarud & Klem for the water of the English Channel. He also found the ratio by weight of iron to phosphorus in the diatoms, obtaining values of 4·2 during the spring outburst and 4·4 later during an outburst of *Rhizosolenia*. Brandt & Raben (1920) had found a high ratio for diatoms in the North Sea, and analyses by T. G. Thompson quoted by Wailes (1929) showed an even higher ratio for diatoms in Puget Sound. Cooper saw the implication of this; it indicated that all the iron in the English Channel water was taken up by diatoms several times during the course of the year.* Thompson & Bremner (1935) actually found a reduction in the quantity of the iron in the water of Puget Sound during the outbursts of diatoms which are exceptionally intense in that area.

* During the course of some 6 weeks in the spring of 1934 in the English Channel, 8 mg. phosphate P were used by the growing diatoms from each cubic metre of water. It follows from Cooper's ratio that some 33 mg. Fe are taken up by diatoms per cubic metre of water. Diatoms containing 8 mg. phosphate P and 33 mg. Fe are not at any time found per cubic metre of water, because more are eaten than are left to form the population. Since the total iron content of the water remained between 25 and 10 mg. Fe per $m.^3$ during this period, it is concluded that iron taken up from the water by diatoms is given back when they are eaten and taken up again when other diatoms develop.

From this knowledge it appeared, and indeed it still seems probable, that the growth of phytoplankton in the sea is at times delayed owing to lack of available iron. Moreover, the growth rate of diatoms in culture was found to be so dependent upon the supply of available iron that reproducible results from experiment to experiment, as distinct from duplicate results in the same experiment, could not be obtained unless iron could be supplied in equally available quantities. It is thought that such experiments on the factors affecting their growth rate will lead to a better understanding of changes taking place in the sea. With these ends in view it was determined to seek information regarding the forms of iron in sea water and the availability of such forms for the growth of phytoplankton.

With regard to the nature of iron occurring in sea water Cooper calculated that less than 10^{-12} mg. per m.^{3} can exist in solution as ferric ions, owing to the great insolubility of ferric hydroxide, once equilibrium had been attained. It was observed early in this investigation that ferric hydroxide slowly gave off ferrous ions into solution even on the alkaline side of neutrality. This led Cooper (1937) to investigate further the "saturation value" of iron ions in sea water. He showed this to be some 10^{-7} mg. per m.^{3} for water at a pH slightly over 8, and to consist for the most part of ferrous and $Fe(OH)^{++}$ ions. He concluded (1935) that the remainder of the iron found in sea water, when equilibrium had been attained, was in the form of hydroxide, mostly as colloidal micelles. Some observations suggest that this view may be subject to a slight, but rather important, modification. It was found that if a precipitate of ferric hydroxide was formed by adding an iron salt to sea water rich in phosphate, the quantity of phosphate in solution was reduced. Further, when sea water containing 87 mg. phosphate P in solution per cubic metre was shaken with freshly prepared ferric hydroxide, the phosphate in solution was reduced to 3 mg. P per m.^{3} in the course of 10 days. Similar observations have been made by Professor S. A. Waksman (private communication). This suggests that part of the iron in natural sea water may be in the form of colloidal ferric phosphate. It was found that various preparations of ferric phosphate sols were more rapidly soluble in dilute acid than hydroxide sols. From this it was inferred that iron phosphate would provide a more rapidly available source of iron for diatoms than hydroxide. Direct experiment has confirmed this.

A considerable body of information exists concerning the formation and properties of ferric hydroxide and similar sols, but this relates to concentrations many hundred times greater than occurs in natural sea water, in which there is only some 3–20 mg. Fe per m.^{3} Direct observations, working down to concentration of 300 mg. Fe per m.^{3}, *suggest* that aggregation of molecules to micelles and subsequent aggregation of micelles to flocs which sediment, is so delayed with increasing dilution, that some very small aggregates may conceivably persist for a long time in natural sea water where the concentration of total iron is far below the limits investigated.

Thus, at the outset, we are provided with a picture of sea water containing iron in the following forms:

(i) Iron in true solution as an equilibrium mixture of ferric, ferrous and $Fe(OH)^{++}$ *ions* amounting in all to some 10^{-7} mg. per m.^{3} If these are present above this equilibrium or saturation value, not only hydrolysis to insoluble ferric hydroxide but intake by diatoms tend to bring their concentration down to saturation value.

(ii) Ferric hydroxide and phosphate as *colloidal micelles and larger aggregates*.

(iii) Stable *organic compounds* of iron, of which there is, as yet, no direct evidence.

As the investigation proceeded, information was obtained bearing upon the following questions: (i) the diffusion of iron ions from the surrounding water as a direct source of supply to diatoms; (ii) adsorption of ferric hydroxide and phosphate on the surface of diatoms; (iii) utilization of particles of ferric hydroxide and phosphate by diatoms; (iv) the quantity of iron needed for growth; and (v) the mechanism by which insoluble particles are used.

Information concerning iron in organic combination in sea water, and the part it plays in regulating the growth of phytoplankton, is left for a further communication.

Calculation of the Maximum Daily Supply of Iron to Diatoms by Diffusion of Iron Ions from the Surrounding Sea Water

It seemed questionable whether diatoms could obtain their requirement for rapid growth from iron ions, even if their "saturation value" of 10^{-7} mg. Fe per m.^{3} was kept up in the diatoms' immediate vicinity by solution from ferric hydroxide particles. There is little more ionic iron in a cubic metre of water than found in a diatom of moderate size. Colloidal particles of ferric hydroxide dissolve only very slowly when the saturation value of ionic iron is raised several thousandfold by making a hydroxide sol slightly acid and the concentration of ionic iron is kept low by adding dipyridyl, acetylacetone or citrate which combine with, and remove from the sphere of action, ferrous or ferric ions.

The question can be investigated in the following manner:

(i) Assuming the most favourable conditions for diffusion of iron ions into the growing cell, the concentration gradient of these ions outside the cell can be calculated. This gives the depth and volume of the zone of water around the cell which is undersaturated with respect to ionic iron.

(ii) The renewal of ions from colloidal micelles of ferric hydroxide takes place in this undersaturated water. By taking a maximum rate at which the particles dissolve, we can arrive at a maximum value of the rate iron ions could diffuse into the cell.

(iii) The quantity of iron taken up daily by a growing diatom can be found and compared with this calculated maximum rate at which it could be supplied from ions in the sea under the most favourable circumstances.

Then, if the quantity taken up daily is greatly in excess of the (possible) maximum daily supply, the calculation provides evidence that the cell obtains iron by some other mechanism than diffusion of ions from the surrounding water.

Proceeding along these lines, it is assumed that iron ions diffuse freely to and through the cell-water interface of the diatom and then at once combine with the cell contents, their concentration on the interior surface of the interface becoming zero.

Consider a spherical living cell of radius r cm. absorbing a solute from a solution at a rate of Q_1 g.-mol. per cm.^{2} per day. In course of time equilibrium will be attained, with a concentration C_∞ of the solute at an (infinite) distance from the cell, becoming zero at the surface.

At a distance x cm. from the centre of the cell the concentric spherical surface A in Fig. 1 is cut by the same cone as the spherical surface S on the cell. Through A will pass, in unit time, the same quantity of solute as passes through S. Since the area of S to A is as r^2 to x^2, $Q_1 . \frac{r^2}{x^2}$ g.-mol. will pass S per cm.^{2} per day.

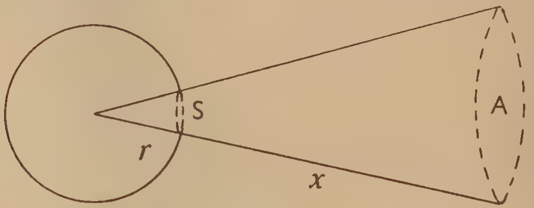


Fig. 1.

Fick's law for diffusion of a solute states $\frac{dC}{dx} = \frac{Q}{Da}$, where Q = quantity of solute in g.-mol. per day diffusing through a boundary of area a cm.^{2}; D = diffusion coefficient (cm.^{2} per day), and dC/dx = the concentration gradient (g.-mol. per litre per cm.).

For a concentric spherical surface at a distance x cm. from the centre of the cell, $\frac{Q}{a} = Q_1 . \frac{r^2}{x^2}$, and hence

$$\frac{dC}{dx} = \frac{Q_1}{D} . \frac{r^2}{x^2}$$

integrating
$$C_x = k - \frac{Q_1 r^2}{Dx},$$

where C_x is the concentration at that boundary.

When x is infinity,
$$C_\infty = k.$$

Hence
$$C_x = C_\infty - \frac{Q_1 r^2}{Dx}. \tag{i}$$

Consider the case where $x = r$ at the surface of the cell, immediately within the cell-water interface where C is postulated as zero

$$C_r = O = C_\infty - \frac{Q_1 r}{D},$$

$$Q_1 = \frac{C_\infty D}{r}, \tag{ii}$$

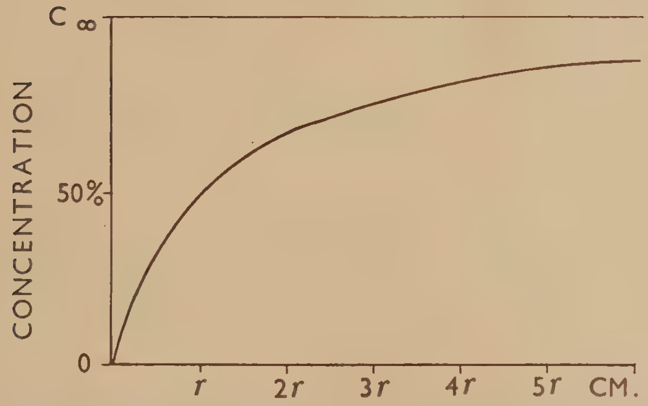


Fig. 2. Diagram showing the concentration of a freely permeable solute at varying distances from a cell, of radius r cm., suspended in water. C_∞ is the concentration at an infinite distance from the cell.

Combining (i) and (ii)
$$\frac{C_x}{C_\infty} = \frac{x-r}{x} \tag{iii}$$

and
$$Q_1 = \frac{xDC_x}{x-r}. \tag{iv}$$

If a spherical living cell of radius r is suspended in water containing a concentration C_∞ of a permeable ion which combines at once on reaching the inner surface of the membrane, then, after a time a state of equilibrium will be attained. When this has taken place equation (iii) gives the concentration in the water at varying distances from the cell and Fig. 2 shows the relation.

Undersaturation to an average extent of about 60% occurs in a zone of water extending $4r$ cm. from the surface of the cell, that is $5r$ from the centre of the cell. For simplicity in calculation it is assumed that at this boundary the concentration (C_{5r}) of iron ions is their saturation value ($1{\cdot}78 \times 10^{-15}$ g.-mol. per litre).

Applying these formulae to a concrete instance of a spherical cell having a surface area $3{\cdot}3 \times 10^{-5}$ cm.^{2} ($r = 1{\cdot}62 \times 10^{-3}$ cm.), the quantity of iron ions entering the surface daily

$$= 3{\cdot}3 \times 10^{-5} . Q_1 \text{ g.-mol.}$$

$$= 3{\cdot}3 \times 10^{-5} \times \frac{5r . D . C_{5r}}{5r - r} \text{ g.-mol. from (iv)}$$

$$= 2{\cdot}8 \times 10^{-17} \text{ g.-mol.}$$

$$\text{or } 1{\cdot}6 \times 10^{-12} \text{ mg. Fe.}$$

The volume of water in the undersaturated zone extending $4r$ from the surface of the cell $= 5{\cdot}25 \times 10^{-7}$ c.c. If this contained 20 mg. Fe as colloidal ferric hydroxide per cubic metre, the total quantity in the undersaturated zone amounts to $10{\cdot}5 \times 10^{-12}$ mg. Fe.

If as much as one-tenth of this dissolved daily in the undersaturated zone, and was able to pass into the cell, in addition to that calculated above, the total daily supply would be

$$2{\cdot}6 \times 10^{-12} \text{ mg. Fe.}$$

The diatom *Lauderia borealis* is a relatively quick-growing species, and in nature a growth rate of one division in 36 hr. would certainly not be excessive (Harvey, Cooper, Lebour & Russell, 1935). A culture of this species, having an average cell-water interface equal to that of the spherical cell considered above, was grown and found to take up from the culture medium $3{\cdot}5 \times 10^{-8}$ mg. phosphate P for each new cell produced. Thus, when growing at the rate of one division in 36 hr., the daily supply per cell would normally be in the order of

$$2{\cdot}2 \times 10^{-8} \text{ mg. phosphate P.}$$

The high ratio of iron to phosphorus found in diatoms indicates that this cell would in nature obtain daily some

$$8 \times 10^{-8} \text{ mg. Fe.}$$

That is over ten thousand times more than the $2{\cdot}6 \times 10^{-12}$ mg. calculation showed it could possibly obtain from iron ions.

A second example provides a check on the magnitude of this result. The diatom *Biddulphia mobiliensis* has been grown in culture at a rate exceeding one division in 36 hr. under a rather wide range of light and temperature conditions. Its surface area approximated to that of a sphere having a radius of 0·0035 cm.

Applying similar calculations to such a sphere, its possible supply from sea water containing 20 mg. Fe per m.^{3} would be 4×10^{-11} daily.

In the mixed diatom community occurring during spring in the English Channel a relation was found (i) between the pigment content of the cells and their phosphorus content (Harvey, Cooper, Lebour & Russell, 1935), (ii) between the phosphorus and iron in the diatoms (Cooper, 1935).

The pigment content of *Biddulphia* cells in culture was found, and from it the iron content of a cell was assessed by applying these two relations. This amounted to $1{\cdot}12 \times 10^{-7}$ mg. or a daily intake of $7{\cdot}5 \times 10^{-8}$ mg. Fe.

The big discrepancies found suggest that diatoms obtain iron by some other mechanism than diffusion of ions from the surrounding water.

It is thought that calculations of this nature do not allow any further conclusions to be drawn for the following reason. Iron is present in diatoms and most living organisms in the ferrous state; hence it is returned to the sea water as ferrous iron, which oxidizes to ferric iron; this hydrolyses to the insoluble hydroxide, the molecules of which aggregate to form particles. There is produced, finally, an equilibrium mixture of ferrous, ferric and $Fe(OH)^{++}$ ions and ferric hydroxide particles. Both processes, oxidation and hydrolysis, take place at very great dilution and so may require a considerable time to reach completion. Hence it is likely that the sea is at times "supersaturated" with ferrous ions. However, such a condition could not persist indefinitely; it could only delay the final formation of hydroxide.

Adsorption of Ferric Hydroxide, and Phosphate, on the Surface of Diatoms

Adsorption compounds are very readily formed by ferric salts with a wide variety of other molecules. The iron atom is ready to accept electrons from other molecules or groups such as hydroxyl which can "donate" electrons. Ferric hydroxide molecules even tend to share electrons with other molecules of ferric hydroxide; thus, on ageing, the hydroxide forms a series of polymers containing finally many atoms of iron (Kolthoff, 1937). It is therefore, *a priori*, to be expected that micelles of ferric hydroxide, and phosphate, will be readily adsorbed upon many and diverse substances.

This was found to be so. The properties of a ferric hydroxide sol were found to be altered by the addition, before, or in some cases even after formation, of a minute quantity of albumen, agar, gum arabic, starch or casein. Such sols, containing sometimes no more emulsoid than iron, when added to sea water did not flocculate for a considerable time, whereas a sol without such emulsoid, when added in similar quantity, flocculates rapidly.

That adsorption of hydroxide takes place on diatoms was suggested in the first place by their high ratio of iron to phosphorus, and by the variable and often high ratio found in published analyses of sea weeds and freshwater algae. In order to obtain evidence concerning this possibility three series of observations were made.

The boundary, or interface, which regulates the diffusion of solutes into the cell and acts as a barrier to colloids is the plasma membrane, of whose lipoid nature there is much evidence. Therefore evidence of adsorption of ferric hydroxide on lipoids was sought.

A sol of ferric hydroxide, containing twice as much gum arabic by weight as iron, was prepared. This was very stable and remained in suspension, when added to sea water, for many weeks. It was added to sea water made faintly opalescent with an emulsion of lecithin, prepared by adding an ether solution of ovolecithin to boiling water. In 2 days the water had cleared and become colourless, the lecithin having adsorbed the ferric hydroxide and sedimented.

The same hydroxide sol was next added to sea water and shaken with a fine emulsion of olive oil. On passing through a filter paper (Whatman No. 42) the filtrate was almost colourless, the hydroxide having been adsorbed on the oil globules which were retained. On filtering the sol in sea water, without addition of oil emulsion, it passed through with little if any adsorption on the filter paper.

These two experiments are interpreted as showing that ferric hydroxide micelles are readily adsorbed on a lipoid surface. Not only were the micelles adsorbed on gum arabic previous to adsorption on the lipoid, but they and the lipoid carried an electronegative charge. The electrostatic repulsion between micelles and droplets was overcome by the forces bringing about adsorption.

The next step was to obtain some direct evidence of adsorption on the living cell. Unfortunately ferric hydroxide micelles, not already adsorbed on an emulsoid, when added to sea water in such quantity that observations can be made, soon flocculate and sediment. Flocculation certainly takes place by preference on diatoms living suspended in the water, indeed to such an extent that spiny and rather transparent species, such as *Chaetoceros*, may appear coated with the brown hydroxide. However, this shows no more than that they act as nuclei on which precipitation takes place by preference.

A sol of ferric hydroxide with gum arabic, as used in the previous experiments, was added to sea water, giving a concentration of 1120 mg. Fe per m.^{3} In one portion of this a bunch of *Fucus*, previously washed in sea water, was placed for a short time. In another portion a similar bunch of *Fucus* was kept for 20 hr., when the iron content of the two waters was compared. A reduction of 12% was found where the *Fucus* had remained overnight.

A sol of ferric hydroxide with starch in place of gum arabic was prepared, containing ten times more starch by weight than iron. This was boiled, to complete hydrolysis of the ferric salt, and was found to remain in suspension when added to sea water for 2 months without flocculation taking place. A quantity amounting to 280 mg. Fe per m.^{3} was added to sterilized sea water, enriched with phosphate, nitrate and silicate. A portion of this was inseminated with *Chaetoceros pseudocurvisetus*. After 6 days part of this, and also of the water which had not been inseminated, was centrifuged, and the following analyses made, using dipyridyl (Cooper, 1935):

N 69. Iron, soluble in boiling HCl (*p*H *ca.* 1·5) in

Diatom suspension	*ca.* 280	mg. Fe/m.^{3}
Centrifugate from diatom suspension	152	,,
,, ,, ,, ,,	129	,,
Water with no diatoms added	280	,,

Hence roughly one-half of the iron hydroxide had been adsorbed on or utilized by the diatoms. Since preliminary oxidation of the suspension with bromine gave no perceptibly greater quantity of iron than solution in hot dilute hydrochloric acid, no large proportion had passed into stable organic combination.

Finally observations were made on diatoms which had been grown in iron rich media and on diatoms from the sea. Ferric citrate to the extent of 560 mg. Fe per $m.^3$ was added to sterilized sea water enriched with nitrate and phosphate, and *Ditylum brightwelli* was grown in this medium, in which ferric hydroxide was in the process of formation. The cells were then stained with acidified ferrocyanide. Small flocs of ferric hydroxide, stained blue, were seen adhering to the diatoms, as would be expected. Further, where the contents had retracted allowing the colour to be seen, the whole cell surface appeared to have taken on a faint blue tint. The same cells were also treated with a saturated solution of dipyridyl in 0·2*N* HCl. Within a minute a red tinge appeared around the periphery of each cell, and the liquid slowly reddened as it does when in contact with ferric hydroxide. In a similar experiment, with *Biddulphia mobiliensis* grown in an iron-rich medium, the whole contents appeared red, and the red compound could be seen streaming from the cells into the surrounding liquid.

Diatom plankton from the sea composed mainly of *Lauderia borealis*, *Biddulphia sinensis* and *Thalassiosira gravida* was concentrated by centrifuging, washed with acetone to dissolve out colouring matter, centrifuged again and suspended in distilled water. A part of this was stained with acid ferrocyanide, and the other part, to which a trace of alizarine yellow was added so that both fluids were the same colour, was used as a control. The walls of the cells stained with ferrocyanide were darker than those in the control, particularly in the case of *Biddulphia* and *Thalassiosira*. The differences were distinct, but not very distinct.

These various observations, no one of which is conclusive, taken together, provide evidence that ferric hydroxide is adsorbed on the surface of diatoms.

Evidence that Particles of Ferric Hydroxide and Phosphate are used by Diatoms

Allen-Miquel culture medium has been used successfully to support the growth of many species of marine diatoms. It is made by adding ferric chloride to sea water enriched with phosphate and nitrate, then adding sodium bicarbonate which brings the hydrogen-ion concentration to *ca.* *p*H 8. A copious precipitate consisting of ferric phosphate with some hydroxide is formed, and it is recorded (Allen & Nelson, 1910) that unless some of this precipitate is retained in the liquid when it is decanted, the fluid will not support the continued growth of diatoms. This observation has since been confirmed by several workers, and is demonstrated in the following experiment.

The diatom *Biddulphia mobiliensis* was added in equal quantity to (i) Allen-Miquel medium freed from precipitate by filtering, (ii) this filtrate with the addition of residue left on the filter paper, and (iii) this filtrate with added ferric citrate to the extent of 400 mg. Fe/m.[3] The three cultures were kept at 17° C. in artificial light for 48 hr., when the number of diatoms in samples from each culture were counted with the following result:

	Percentage increase in 48 hr.
In filtrate from Allen-Miquel medium	36
,, ,, ,, ,, +residue	132
,, ,, ,, ,, +400 mg. Fe/m.[3] as citrate	100

Two experiments were made in which sterilized sea water enriched with phosphate nitrate and silicate was inseminated with *Chaetoceros pseudocurvisetus* growing actively in culture. A ferric hydroxide sol was prepared by adding ferric chloride to a slight excess of sodium hydroxide, the colloidal solution having a *p*H *ca.* 9. The effect of adding this (final concentration 280 mg. Fe per m.[3]) was to discolour the suspended diatoms with ferric hydroxide and bring about in 10 days a considerable growth, as compared with the control to which no iron had been added. At the same time a similar sol had been prepared containing ten times more starch than iron. This was boiled, a treatment calculated to complete hydrolysis of the iron salt as it both increases the rate of reaction and temporarily raises the hydroxyl ion concentration to a high level. The addition of the same quantity of iron in this form to the diatom suspension did not give any perceptible deposition of ferric hydroxide on the diatoms, but it did bring about a considerable growth. This was judged to be as great as that due to the addition of the same quantity of iron in the form of citrate, and slightly less than that due to the same quantity of iron in the form of the sol without starch, which settled out on the diatoms.

For the second experiment a similar alkaline sol was prepared, but it was boiled before use; also a similar alkaline sol, containing starch, which was twice brought to boiling-point before use. Each was added to the diatom suspension to the extent of 560 mg. Fe per m.[3] A rich growth compared with that in the controls was obtained in both cases; the growth in both was slightly greater than that where the same quantity of iron had been added in the form of citrate.

These two experiments indicate that ferric hydroxide particles of colloidal or of larger size were utilized by the diatom.

The diatom *Nitzschia closterium* var. *minutissima* is particularly suitable for experiments on iron intake, since its growth may be brought almost to a standstill through lack of iron without apparent injury. The cells are then pale in colour but grow rapidly on adding iron. A series of experiments has been made by transferring such cells in equal quantity to sterilized sea water, enriched with phosphate, nitrate and silicate, with and without added iron in various forms:

Exp. 62. A culture of *Nitzschia*, in which growth had ceased and the cells were yellow green in colour, was used for insemination. Additions of 280 mg. Fe per m.[3]

were made with ferric citrate; hydroxide sol freshly prepared; hydroxide-gum arabic sol (Fe : gum :: 1 : 2), *p*H *ca.* 9; the same after boiling; hydroxide-starch sol (Fe : starch :: 1 : 10) boiled.

After 7 days the greatest growth was in the flasks enriched with citrate and freshly prepared hydroxide sol, the least in flasks enriched with boiled alkaline hydroxide-gum arabic sol. In all the flasks with added iron there was more growth than in the control.

After 20 days the increased growth due to the various forms of added iron was indistinguishable.

Exp. 64. The same subculture of *Nitzschia* was used and additions of 280 mg. Fe per m.^{3} made with ferric citrate, with a hydroxide-starch sol (Fe : starch :: 1 : 10) at *p*H 8·5, and with the same after it had been boiled, also at *p*H 8·5.

During the first week, the most rapid growth occurred with citrate and the least rapid increase in growth with boiled sol.

After 18 days there was little or no difference between the growth in the flasks with added iron.

Exp. 67. The yellow-green *Nitzschia* had meanwhile been transferred to sterilized sea water and was actively growing when used for insemination. Additions of 280 mg. Fe per m.^{3} were made with citrate, hydroxide sol, the same boiled, hydroxide-agar sol. All the sols were at *p*H *ca.* 9.

No difference in growth rate could be distinguished, and after 13 days a considerable and similar production of diatoms had taken place in all the flasks to which iron had been added.

A further addition of iron citrate at this stage brought about no increase in diatoms, but a further addition of nitrate and phosphate caused a 50 % increase in the crop after a further 10 days.

These experiments again indicate that colloidal and larger particles of ferric hydroxide, if in considerable quantity, can be utilized by diatoms. The amount added—280 mg. Fe per m.^{3}—is over ten times more than ordinarily occurs in the sea, but the diatom population in these cultures is itself many times more than ordinarily occurs in the sea.

The effect of adding sols in very *small* quantity was then investigated. In the first series of experiments sols were made in alkaline solution at a concentration of 0·001 *M* with respect to iron. These were boiled, a process which probably both completes hydrolysis and gives rise to rather large colloidal aggregates. They were then diluted to 0·000005 *M* and added to the *Nitzschia* suspensions.

Concentration of iron in the culture due to addition:

2·8	mg. per m.^{3}	as	ferric hydroxide sol.
5·6	,,	,,	ferric hydroxide sol.
2·8	,,	,,	ferric hydroxide-starch sol.
11·3	,,	,,	ferric phosphate sol.

In every case a perceptibly greater growth occurred than in the control with no added iron; and always the increase in diatoms was considerably less than that due to the addition of the same quantity of iron in the form of citrate. This considerable difference was thought to be due to the size of the micelles in these sols, made in a relatively concentrated form and then boiled, compared with the size of micelles in process of formation at very great dilution from citrate.* This view gains confirmation from the following experiment.

Exp. 106. Additions of iron to flasks of *Nitzschia* suspension, in each case amounting to 5·6 mg. Fe per m.^{3}, were made with the following freshly prepared sols:

Ferric hydroxide sol (*C*) made by adding $M/250$ ferric nitrate to an equal volume of $4N/250$ sodium hydroxide and then diluting to $M/200{,}000$ with respect to iron.

Ferric hydroxide sol (*D*) made by adding $M/100{,}000$ ferric nitrate to an equal volume of $4N/100{,}000$ sodium hydroxide.

Ferric phosphate sol (*C*) made by adding $M/250$ ferric nitrate to an equal volume of $M/250$ Na_2HPO_4 and diluting to $M/200{,}000$.

Ferric phosphate sol (*D*) made by adding $M/100{,}000$ ferric nitrate to an equal volume of $M/100{,}000$ Na_2HPO_4.

At the same time, the same quantity of iron was added to flasks of the *Nitzschia* suspension in the form of citrate, ferrous dipyridyl, and iron-ascorbic acid complex. The two latter compounds hydrolyse in sea water less rapidly than the citrate.

Growth was most rapid in the flasks with iron added as phosphate sols, ferrous dipyridyl and the ascorbic complex, less rapid in the flasks with ferric hydroxide sol (*D*) and citrate, least rapid with ferric hydroxide sol (*C*). Very little growth took place in the control.

After 26 days, a similar increase had taken place in all flasks with added iron (*ca.* $3{\cdot}68 \times 10^{12}$ cells per m.^{3}) with the exception of the hydroxide sol (*C*), where there was, by inspection, rather less and where many of the cells were misshapen and matted together.

THE QUANTITY OF IRON NEEDED FOR GROWTH BY DIATOMS

Four experiments have been made to determine the increased number of *Nitzschia* cells which develop in culture due to the addition of small quantities of iron.

	Addition	Increase in number of cells compared with control, due to addition of 1 mg. Fe
N 82	2·8 mg. per m.^{3} as citrate	$4{\cdot}3 \times 10^{12}$
	5·6 ,, ,, ,,	$2{\cdot}4 \times 10^{12}$
1933	2·0 ,, ,, ,,	3×10^{12}
	5·0 ,, ,, ,,	4×10^{12}
N 109	2·8 ,, ,, ,,	$1{\cdot}8 \times 10^{12}$
N 106	5·6 ,, ,, phosphate	$3{\cdot}7 \times 10^{12}$
	Mean value	$3{\cdot}2 \times 10^{12}$

Since it is improbable that all the iron added was actually used and passed into the cells of the diatoms, these experiments indicate that 1 mg. of iron is contained in more than 3×10^{12} cells.

Similar experiments were also made to determine the increase in numbers due to the addition of phosphate to cultures rich in nitrate but poor in phosphate, with the following results:

---

* Iron citrate hydrolyses in sea water. The citrate stabilizes ferric hydroxide particles of colloidal size, delaying their flocculation and precipitation. Thus a mixture of ferric chloride and citrate does not give a precipitate on adding to sea water for some hours, whereas ferric chloride alone does so.

	Increase in number of cells, compared with control, due to addition of 1 mg. P
Exp. N 83	14×10^9
	$10{\cdot}5 \times 10^9$
Exp. N 95	28×10^9
	21×10^9
Mean value	$18{\cdot}4 \times 10^9$

Hence, on the average, 1 mg. Fe and 175 mg. P caused similar increases in diatom population.

This leads to the inference that less iron than $\frac{1}{175}$th of the phosphorus content was actually needed within the cell, although several times more iron than phosphorus is usually found in and on diatoms in nature.

The diatom *Nitzschia* is not only a pennate species but behaves differently in culture from centric species. Since it would be dangerous to generalize from experiments on *Nitzschia* alone, the following experiment was made.

Sea water enriched with phosphate nitrate and soil extract was inseminated with *Lauderia borealis* and kept until the growth of diatoms had utilized 360 mg. phosphate P per m.^{3} The total quantity of iron in the culture, fluid + diatoms, was then determined. This amounted to 25 mg. Fe per m.^{3} Hence the ratio of iron to phosphorus used by the diatoms was at most 25/360, probably much less, since much of the iron was, doubtless, not within the diatom cells.

SUGGESTED MECHANISM BY WHICH DIATOMS UTILIZE FERRIC HYDROXIDE AND PHOSPHATE ADSORBED ON THEIR SURFACE

In the pennate diatoms protoplasm streams out through holes from the interior of the cell, moves over the skeleton and passes into the cell again through other holes; a fresh surface of protoplasm is more or less continuously being exposed to the water. The centric diatoms have many small pores in the skeleton exposing the protoplasm, and there is evidence (Schütt, 1899) that it extrudes to form a film on the exterior of the skeleton. The cell sap is acid in reaction; Dr F. Gross (unpublished data) found a *p*H of about 4·5 by crushing diatoms in an unbuffered fluid with indicators. The cell contents, in common with other living cells, probably have a low oxidation-reduction potential.

The free diffusion of colloids into the cell is barred by the "plasma membrane" situated at or close to the exterior surface of the protoplasm.* It is the effective diatom-water interface with regard to the free diffusion of solutes and ions into and out of the cell. Since growing cells can build up a concentration of some particular ion many times greater than in the surrounding water, work is done in concentrating the ion. From impedance measurements Cole (1928) suggests that the thickness of the membrane may be even less than monomolecular, and that the transfer of ions into the cell may be largely due to electrostatic forces at this surface.

---

* This statement may conceivably require qualification. East & White (1933) obtained some evidence that colloid particles of small size may pass a plasma membrane. Marklund (1936) observed that large molecules penetrate into the cell of the diatom *Melosira* more readily than into most vegetable cells.

From these considerations it seems clear that ferric hydroxide particles, adsorbed on the surface of a growing diatom, are just where considerable changes in energy are normally taking place.

It is almost unanimously conceded that lipoids occur at this surface, where they would be so orientated that their carboxyl groups are exposed to the water. At such an interface the hydrogen-ion concentration can be different from that in the main body of water.

Danielli (1937) has calculated that this difference may amount to as much as two units of *p*H.

Hence there is reason to suppose that adsorbed particles of ferric hydroxide are upon a seat where their solution and passage into the diatom is possible, indeed imminent.

SUMMARY

The nature of iron occurring in sea water, and its utilization by diatoms, is discussed.

Diatoms in the sea obtain many thousand times more iron than calculation shows they can obtain by diffusion of iron ions from the surrounding water.

Evidence is presented that ferric hydroxide is readily adsorbed on the surface of diatoms.

It is shown that colloidal and larger particles of ferric hydroxide or phosphate can be utilized by, and support the growth of diatoms.

Experiments show that the diatoms *Nitzschia closterium* and *Lauderia borealis* require, for continued growth, a very small quantity of iron compared with that found on, and in, diatoms taken from the open sea.

It is contended that iron hydroxide adsorbed on diatoms is in contact with an interface where its solution, and subsequent passage into the cell, is probable.

The co-operation of Dr L. H. N. Cooper, who investigated the equilibrium between iron ions and oxidation-reduction potential in sea water, has been invaluable. I am also indebted to Dr Fabius Gross for cultures of diatoms and much information, to Mr G. M. Spooner for statistical analyses of counts of diatoms made in connexion with this enquiry and to Dr W. R. G. Atkins for reading the manuscript.

REFERENCES

ALLEN, E. J. & NELSON, E. W., 1910. Artificial culture of marine plankton organisms. *Quart. Journ. Micr. Sci.*, Vol. 60, p. 361.

BRAARUD, T. & KLEM, A., 1931. Hydrographical and chemical investigations in the sea off Möre. *Skr. uttgift av Hvalrådets ved Univ. Biol. Lab. Oslo*, No. 1.

BRANDT, K. & RABEN, E., 1920. Zur Kenntnis der chemischen Zusammensetzung des Planktons. *Wiss. Meeresuntersuch., Abt. Kiel*, N.F., Bd. 19, pp. 175–210.

COLE, K. S., 1928. Electric impedance of suspensions of *Arbacia* eggs. *Journ. Gen. Physiol.*, Vol. 12, p. 37.

COOPER, L. H. N., 1935. Iron in the sea and in marine plankton. *Proc. Roy. Soc.*, B, Vol. 118, p. 419.

—— 1937. *Proc. Roy. Soc.*, B (in press)

DANIELLI, J. F., 1937. Surface *p*H, ion concentration and interfacial tension. *Proc. Roy. Soc.*, B, Vol. 122, p. 155.

EAST, E. M. & WHITE, B., 1933. Reactions of *Valonia* to colloids. *Journ. Gen. Physiol.*, Vol. 16, p. 925.

GRAN, H. H., 1931. On the conditions for the production of plankton in the sea. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. 75, p. 37.

HARVEY, COOPER, LEBOUR & RUSSELL, 1935. Plankton production and its control. *Journ. Mar. Biol. Assoc.*, Vol. XX, p. 407.

KOLTHOFF, I. M., 1937. Ageing of fresh precipitates. *Proc. Kon. Akad. van Wet. te Amsterdam*, Vol. 40, p. 82.

MARKLUND, 1936. *Acta Bot. Fennica*, Vol. 18, p. 1. Quoted by Collander, R., 1937. Permeability. *Ann. Rev. Biochemistry*, Vol. 6.

SCHÜTT, F., 1889. Centrifugales dickenwachstum der Membranen und extramembranoses Plasma. *Jahr. Wiss. Bot.*, Vol. 33, p. 1.

SEIWELL, G., 1935. Note on iron analyses of coastal Atlantic waters. *Ecology*, Vol. 16, p. 663.

THOMPSON, T. G. & BREMNER, R., 1935. The occurrence of iron in the water of the N.E. Pacific Ocean. *Journ. Cons. Int. Expl. Mer*, Vol. X, p. 39.

WAILES, G., 1929. Plant life in the open sea. *Museum and Art Notes, Vancouver*, Vol. 4, p. 83.

NOTE ON COLLOIDAL FERRIC HYDROXIDE IN SEA WATER

By H. W. Harvey, Sc.D., M.A.

Hydrographer at the Plymouth Laboratory

If a sol of colloidal ferric hydroxide is added to sea water, or if the hydroxide is formed in sea water by adding a solution of an iron salt, the aggregated molecules of hydroxide coalesce to form flocs which fall rather rapidly as a precipitate. When several thousand mg. of iron are added per cubic metre of sea water, flocculation is immediate; on adding 300–500 mg. Fe per $m.^3$ in sufficiently dilute solution (10^{-4} or $10^{-5} M$) flocculation and sedimentation may be delayed for several days. Although this quantity is over twenty times as much as ordinarily occurs in the sea, it seemed rather remarkable that the waters of the open ocean could maintain any material quantity of ferric hydroxide in suspension, since it would there have many years in which to flocculate and fall.

Waksman had suggested that much of the iron in sea water may be in the form of iron humates derived from the breakdown of organisms, and he had obtained evidence that such humates were compounds of lignoproteinates.

Since ferric hydroxide in sea water, in spite of its great insolubility, is utilized by diatoms, some experiments concerning its nature were made, and an account of some of these may be of use to others interested in the same field.

Colloidal Ferric Hydroxide adsorbed on Emulsoids

A number of sols have been prepared by adding $M/500$ ferrous or ferric salts containing a small quantity of various emulsoids to an equal volume of sodium hydroxide, of such concentration that the resultant liquid was alkaline (pH 8–10).

Sols prepared in this way and containing one to eight times more *gum arabic* by weight than iron, when added to sea water, giving a final concentration of 2000–5000 mg. per $m.^3$, did not flocculate for several weeks. They also gave a clear solution in normal sodium hydroxide.

Sols containing four to ten times more *starch* by weight than iron when added to sea water did not flocculate for several days. On standing or boiling, the sols darken in colour with a rise in hydrogen-ion concentration, suggesting that hydrolysis is not completed for some time even in such alkaline media. Boiled sols containing ten times more starch than iron when added to sea water did not flocculate for many weeks, and gave a clear solution in normal sodium hydroxide.

Sols containing two to ten times as much *albumen* as iron, when added to sea water, remained in suspension for some hours or days.

Sols containing two to four times as much *agar-agar* as iron when added to sea water did not flocculate until after 2 or 3 days. The precipitate formed then appears more voluminous and, after shaking, it settles less rapidly than a precipitate formed from an equivalent quantity of iron salt, or sol, without emulsoid. A notable instance of this occurred on adding such a sol to sea water to the extent of 2240 mg. Fe and 8000 mg. agar per m.[3] Flocculation and sedimentation were observed after 3 days; a week later, when sedimentation appeared to be complete, the flask was shaken, and thereafter much of the precipitate remained in suspension throughout a period of 2 months. The experiment was repeated.

In order to account for an emulsoid "protecting" a sol from flocculating in a solution of an electrolyte, a theory has been advanced that the emulsoid forms a shell around the irreversible colloidal particle. The presence of this shell prevents the particles coalescing by either (i) offering a material obstacle or (ii) preventing the cause which brings about coalescence of the particles, that is the loss of their electric charges (Burton, 1916, p. 170). The degree of protection is attributed by Freundlich (1925, p. 125) to the "uniformity, closeness and solidity" of the shell or envelope of emulsoid.

In all the instances examined protection has been given to many molecules of ferric hydroxide by a single molecule of emulsoid. Even with ten times less iron, there will be many more molecules of ferric hydroxide than emulsoid, owing to the very high molecular weight of the latter. This indicates that a shell of emulsoid was not formed round the hydroxide.

In addition to altering the tendency of colloidal hydroxide to flocculate, it was observed that small quantities of emulsoid also reduced the rate at which the colloidal hydroxide dissolved in dilute acids or in sodium citrate.

Cooper's investigations (1935) have shown that iron in the sea is probably taken up by phytoplankton and given back to the water several times in the course of a year. When unicellular plants are eaten, broken and defaecated by zooplankton, or die, iron released from organic combination will be hydrolysed in the alkaline sea water. This takes place in the presence of organic matter—the protein of the diatom, its surrounding slime, etc.—so a certain measure of protection may be expected. Colloidal particles of iron hydroxide adsorbed upon the plant (Harvey, 1937) are also likely to be set free in a more or less "protected" state.

It seems therefore that two factors tend to keep ferric hydroxide in colloidal suspension in the sea, their very low concentration and their "protection".

If flocculation takes place, sedimentation of an unprotected sol proceeds more or less rapidly. In the open ocean, at a distance from the land, the upper layers are beyond the influence of land drainage, and where marked layering exists, any considerable renewal of their iron content from below would seem improbable. In wide expanses of ocean in the tropics, the water remains in the upper warmer layers for several years, time enough for flocculation and sedimentation of unprotected ferric hydroxide to take place and to leave the water iron-free, and in consequence barren of plant life, but not *necessarily* barren of phosphates and nitrates. This would only occur if turbulence did not keep the upper layers supplied with (flocculated) particles from below. That turbulence may be sufficient to do this, in spite of layering, is suggested in Seiwell's (1935) interesting conclusions concerning the vertical transference of phosphate and oxygen in the open ocean.

Iron Humates

Waksman (1932) has suggested that much of the iron in sea water may be in combination with humic substances, and he has shown that "natural" humic acids are very similar to lignoproteinates in composition, in properties, and in resisting bacterial attack. Both combine with or adsorb iron salts, in small amount compared with their own weight, and give a product which dissolves in alkali to a clear solution.

A few observations were made on iron-containing compounds of this nature.

(i) Ferric chloride was added to *lignin*. The product was soluble in dilute sodium hydroxide, but on raising the concentration to 0·5 *N*, ferric hydroxide precipitated.

(ii) Ferric chloride and a small quantity of *peptone* were added to *lignin*. The product, soluble in dilute alkali, gave a clear solution in normal sodium hydroxide. It was partly precipitated in sea water.

(iii) Ferric chloride was added to "*humic acid*", prepared from peat by repeatedly dissolving in alkali and precipitating with acid. The product gave a clear solution in normal sodium hydroxide and was partly precipitated in sea water.

(iv) I am indebted to Prof. S. A. Waksman for a preparation of *ligno-caseinate* containing almost 2 % of iron, similar to that used by Gran (1933) as a source of iron for the growth of diatoms. It resembled the peat humic acid and the lignin-peptone products in giving a clear solution in strong alkali and in being partly precipitated in sea water. After several weeks sea water was found to have retained in solution 5 % of the iron added in this form. (I am indebted to Dr L. H. N. Cooper for making estimations of the iron remaining in solution.)

The following experiment suggests that it is the iron remaining in solution which is utilized by diatoms.

N 12. Growth of *Biddulphia mobiliensis* in cultures containing iron as Waksman's artificial humate and as ammonium ferricitrate, added to water enriched with phosphate nitrate and silicate.

	% increase of diatoms
Sea water enriched N, P, Si, with 400 mg. Fe/m.^{3} as artificial humate added 20 days previous to insemination	327
Filtrate from above	317
Sea water enriched N, P, Si with 400 mg. Fe/m.^{3} as ammonium ferricitrate added 20 days previous to insemination	480
Filtrate from above	96
Filtrate from above + 400 mg. Fe/m.^{3} as citrate	612

The result of this experiment was confirmed.

In experiments with *Nitzschia closterium* it was observed that addition of the ligno-casein product caused less rapid growth than iron citrate or hydroxide sol when added in amounts containing the same quantity of iron. With small additions—5·6 mg. Fe per $m.^3$—its effect was much less.

THE ELECTRIC CHARGE ON COLLOIDAL PARTICLES OF FERRIC HYDROXIDE

Powis (1915) found that colloidal particles in a strongly alkaline sol (0·002 N NaOH) carried an electronegative charge, and in an acid solution a positive charge. The polarity could be changed by suitably changing the reaction. He did not investigate the iso-electric point.

A ferric hydroxide sol was prepared having a pH *ca.* 7·4 and the particles were found to carry an electropositive charge, moving towards the negative electrode in a cataphoresis tube at 5×10^{-5} cm. per volt per sec.

On the addition of four times as much gum arabic (an electronegative emulsoid) as there was iron, the polarity changed, the particles moving towards the positive electrode at $11 \cdot 8 \times 10^{-5}$ cm. per V. per sec.

When diluted with an equal quantity of sea water, this protected sol was found to have retained part of its electronegative charge, moving at *ca.* $3 \cdot 7 \times 10^{-5}$ cm. per V. per sec.

Two other sols were prepared, containing respectively twice and four times as much gum arabic as iron, added previous to the formation of hydroxide. In both experiments the colloid particles were electronegative, in the latter moving at 11×10^{-5} cm. per V. per sec. and, after mixing with an equal volume of sea water, at *ca.* 6×10^{-5} cm. per V. per sec.

A second instance of change of polarity to that of the emulsoid was found on adding gum arabic to dialysed iron.

Albumen in a ferric hydroxide sol delays its flocculation in sea water. This emulsoid is electronegative in alkaline solution and electropositive in acid solution (Hardy, 1899). An alkaline sol containing five times as much albumen as iron was found to be electronegative, moving at 10×10^{-5} cm. per V. per sec., while an acid sol prepared by adding albumen to dialysed iron was found to be electropositive, moving at 4×10^{-5} cm. per V. per sec. When mixed with sea water, no movement in an electric field could be detected, although a definite measure of protection had been afforded. This was also the case with an electronegative sol containing agar-agar. The method would not have allowed a small charge, remaining on the particles when in sea water, to have been detected.

SUMMARY

Colloidal ferric hydroxide flocculates in sea water, the less rapidly the greater the dilution. When formed in the presence of very small quantities of various emulsoids, it does not flocculate on adding to sea water or flocculates less rapidly.

Many molecules of ferric hydroxide are adsorbed on and "protected" by one molecule of emulsoid. The shell theory of protection does not apply.

It is probable that ferric hydroxide in the sea is similarly adsorbed on emulsoids.

The nature and behaviour of iron humates is considered.

The electric charge carried by colloidal particles of ferric hydroxide has been determined, and it is found that when adsorbed on gum arabic, albumen or agar-agar they had the same polarity as the emulsoid.

REFERENCES

BURTON, E. F., 1916. *The Physical Properties of Colloidal Solutions*. London.
COOPER, L. H. N., 1935. Iron in the sea. *Proc. Roy. Soc.*, B, Vol. 118, p. 419.
FREUNDLICH, H., 1925. *The Elements of Colloidal Chemistry*. London.
GRAN, H. H., 1933. Distribution of phytoplankton in the Gulf of Maine. *Biol. Bull.*, Vol. 64, p. 159.
HARDY, W. B., 1899. On the coagulation of proteid by electricity. *Journ. Physiol.*, Vol. 24, p. 288.
HARVEY, H. W., 1937. The supply of iron to diatoms. *Journ. Mar. Biol. Assoc.*, Vol. XXII, p. 205.
POWIS, F., 1915. Negative colloidal ferric hydroxide. *Journ. Chem. Soc.*, Vol. 107, p. 818.
SEIWELL, H. R., 1935. The annual organic production and nutrient salt requirements in the tropical western North Atlantic. *Journ. Cons. Int. Expl. Mer*, Vol. X, p. 20.
WAKSMAN, S. A., 1933. Marine humus. *Soil Science*, Vol. 34, p. 125.
WAKSMAN, S. A. & IYER, K., 1932. Synthesis of a humus nucleus. *Journ. Wash. Acad Sci.*, Vol. 22, p. 41.

THE INFLUENCE OF THE SUBSTRATUM ON THE METAMORPHOSIS OF *NOTOMASTUS* LARVAE

By Douglas P. Wilson, M.Sc.

Naturalist at the Plymouth Laboratory

CONTENTS

	PAGE
Introduction	227
Methods	229
The Stages of Metamorphosis	230
Note on Tube Building	231
Descriptions of the Experiments and their Results	231
Discussion of the Results	240
Summary	242
References	243

INTRODUCTION

Among the factors responsible for local distribution of the marine bottom fauna it is well known that the nature, particularly the grade, of the bottom deposit is all important. Mud, for instance, yields quite a different animal association from sand or gravel. Many, if not most, of the animals concerned have pelagic larvae, which drift with the plankton during early development, and the question at once arises how, when the time comes to metamorphose, larvae reach the kind of substratum to which their adult lives are suited.

It has been answered by supposing that, like seeds scattered by the wind, they take their chance of falling on to either barren or fruitful soil. Thus in a recent paper Yonge (1937, p. 699), while discussing the distribution of two closely allied species of *Aporrhais*, one of which lives in firm muddy gravel bottoms, the other in softer bottoms of fine mud, has suggested that "the survival of the young of the two species, after they descend at metamorphosis from the surface waters, must depend on the type of bottom on which they fall etc." If they drop on to the right kind of bottom they survive, if not they die.

Now this idea, which seems to have been accepted generally by many writers—unconsciously perhaps and not necessarily stated neatly and specifically as by Yonge—presupposes that metamorphosis takes place in mid-water and that after sinking to the bottom the young molluscs, worms, or whatever they may be are not able to rise up and swim again; they have no chance of getting away should the soil not be to their liking. Yet we know that often there is produced about the time of metamorphosis a creature that can both crawl and swim. Lebour, for example, has definitely recorded this (1931–6) for veligers of the following species: *Nassarius reticulatus*, *N. incrassatus*, *Philbertia gracilis*, *P. linearis*, *Erato voluta*, *Rissoa parva*, *Natica maculata*, *N. catena*. Such a stage doubtless occurs in many other molluscs, as well as in the development of species belonging to other phyla, and it is likely that if larvae in this stage strike an unsuitable substratum they will rise and swim away, drifting perhaps with the currents to new ground. Even if they possess this ability for a few days only their chances of ultimately reaching a satisfactory soil are enormously increased compared with those of inert seeds, which once fallen cannot move of their own volition.

The rate at which a species develops is generally considered to be fairly constant at a given temperature within the normal range, though variations do occur, depending doubtless on such factors as the relative amounts of food individual larvae obtain. One might expect that metamorphosis would take place when a fairly constant and predictable interval of time had elapsed after fertilization, in other words that it is a phase of development which must supervene once a definite stage has been reached. If this were so the risks attendant on settlement would be greater than they probably are; the larvae would have to strike the right grade at a definite instant in their development, particularly so if the transition from a swimming organism to one that can only burrow or crawl be at all rapid. Cataclysmically metamorphosing larvae, however, can probably undergo the change at any convenient moment during a period of several days at least; I have already shown that this is true for *Owenia fusiformis* (Wilson, 1932). Species with a more gradual metamorphosis may be able to delay the event for a long period as can *Scolecolepis fuliginosa* (Day & Wilson, 1934). With cultures of *Branchiomma vesiculosum* (Wilson, 1936) a fairly suitable substratum was available all the while, but there was considerable variation in the time of settling. In this instance, however, we do not know whether each larva metamorphosed as soon as it was able, or whether, as seems probable, some delayed for a time because conditions in a bowl are not ideal.

The investigation of problems concerning the settlement of larvae is of no little importance in the study of distribution and may be of economic importance, as in the oyster and wood-boring organisms. Among the more outstanding papers which have already appeared may be mentioned that of Grave & Woodbridge (1924) on the influence of light and shade in directing the larvae of *Botryllus* to a resting place, Visscher's work (1928) and that by Visscher & Luce (1928) on the settling of *Balanus* cyprids, and the paper by Prytherch (1934) dealing with the surprising role of copper in the settling of the American oyster. Davis (1923), from a somewhat different aspect, has discussed the influence of currents on the dispersal and chances of settling of the larvae of *Spisula*, a staple food of the plaice. On the whole, however, little has been accomplished, and our knowledge of the reactions of larvae to the grade of the bottom deposit is especially scanty. We have also very few data on the ability or otherwise of larvae to postpone metamorphosis until a favourable substratum is reached.

With the intention of continuing investigations along the lines indicated at the end of the last paragraph it was decided to test the larvae of *Notomastus latericeus* Sars. The development of this species has already been described (Wilson, 1933); fertilizations are readily obtainable and the larvae easily reared. They seemed to be specially suitable for the purpose in that they do not feed until some days after metamorphosis, and there are therefore no complications due to introduced food materials. The adults, moreover, are generally confined to mud and very muddy sand, although they are occasionally to be found in somewhat cleaner situations. They do not occur in clean coarse sand or gravel. Pelagic life is, however, rather short, so any postponement of metamorphosis might be of very brief duration. The larvae are also very small and might be difficult to find in the mud after settling. As it turned out this last was by far the greatest difficulty encountered.

METHODS

Adult worms were dug out of the mud at the Salstone, Salcombe, and fertilizations were made as described in a previous paper (Wilson, 1933). Larvae were generally reared in a plunger-jar for a few days before the experiments were set up. The small dishes used in these experiments were covered with glass plates and stood on a bench close together so that lighting and temperature conditions should be as uniform as possible throughout each experiment. Details of the various dishes are given below. The sea water used was taken from well outside the breakwater and was invariably passed through a Berkefeld filter. All gravels, sands and muds were sterilized by boiling in fresh water and then thoroughly washed with repeated changes of filtered sea water.

The mud used was that in which the adults were found. It contained a fairly high proportion of sand grains which varied in size between about 40 and 2000 μ. The main body consisted of flocculent matter from very fine particles to small masses of soft material. In the dishes it settled a little unnaturally in that the finest particles deposited last of all to form a film over the surface. In nature the surface showed a higher proportion of exposed sand grains, the finest particles evidently washing away at the surface. I do not think, however, that this difference had any real effect on the settling of the larvae. The clean sand had a more uniform particle size than the mud: the greatest diameter of the grains generally lay between 100 and 500 μ, very few were smaller or larger than this, while the average size worked out at 243 μ. There was no contained flocculent matter. The gravel, a moderately coarse clean gravel of shell fragments from deep water, was well washed to remove all fine particles. The remaining fragments varied in size from about 500 to 8000 μ along their greatest lengths: the average was approximately 3000 μ.

The larvae when they settled were about 300 μ long, and as already mentioned the chief difficulty was to find them in the soils. Searching the latter was a tedious process tiring to the eyes. A little mud or sand would be removed from the experimental dish and dispersed under water in a glass trough on the stage of a binocular dissecting microscope. As the newly settled larvae were smaller than many of the sand grains they were difficult to detect until they moved. They were most easily found in the clean sand, especially when they had formed their first rough tubes. In the mud the great variety of debris tended to conceal even these tubes. Settled larvae were also very difficult to find in the gravel where the fragments were so much larger than they. If after searching a dish intensively for 1–2 hr. the majority of the larvae or worms had been found, and their various conditions noted, the result was considered sufficiently good for the purpose. The last few were naturally the most difficult to find, and their condition, whatever it was, would not upset the main conclusion. When larvae were not found it must not be assumed that they had died, because during the first week or 10 days the death-rate of this species, even in crowded finger-bowls, was negligible. The larvae are very hardy and have been known to survive for many hours after severe injuries.

On account of the time taken to search one dish thoroughly it was not usually possible to examine all of them properly on any one day, although it could quickly be seen whether any larvae were still swimming or not, and this much at least would be recorded.

The Stages of Metamorphosis

For our present purpose metamorphosis can be divided conveniently into three stages. In the first the larva attaches itself to the substratum by its posterior end, gland cells in the pygidium producing some sticky substance which enables it to do this. At first the adhesion is slight and the larva readily swims away if disturbed; it may break away of its own accord, as often happened in the clean controls. The cilia of both prototroch and telotroch beat strongly, there are no signs of their coming disappearance. This, the "sticky stage", is represented in the tables by the letter *b*, letter *a* denoting freely swimming larvae.

The second stage begins when prototroch and telotroch start to disappear and lasts until metamorphosis is practically completed. This stage is denoted by the letter *c*.

In the third stage the worms have completed metamorphosis, either just finished or any time afterwards; they are indicated by the letter *d*.

This classification is on very broad lines, but it is ample for the purpose and any finer divisions are unnecessary. It should be noted, however, that metamorphosis is considered as being completed with the final disappearance of prototroch and telotroch. No attention is paid to the neurotroch which is got rid of a little later; it was not practicable to determine the condition of that organ without considerable extra work for which time was not available.

NOTE ON TUBE BUILDING

In my 1933 paper no mention is made of the tube these worms build when they first settle down; they were not at that time specially provided with mud or sand as in these experiments. The metamorphosing worm quite early sticks together sand grains or debris into the form of a rough fragile tube. The process begins at the time when the larva first anchors itself by the pygidial glands, and the grains are soon loosely knit into the form of a tube. If the tube is disturbed or broken shortly after its formation the larva will release itself and swim away. Such larvae are always recorded in the tabulated results as stage *b*. The tubes are quite short at first, during the first day or two about a millimetre long and half that in width. Later they reach lengths of several millimetres. The mucus used in the construction of the tubes is probably secreted by ectodermal glands of the body wall and of the pygidium, but the point has not been definitely settled. Sometimes the worms are found out of their tubes crawling freely in the sand or mud.

DESCRIPTIONS OF THE EXPERIMENTS AND THEIR RESULTS

The first set of experiments was made with larvae from eggs fertilized on May 2 1935. The larvae were reared in a plunger-jar until May 7, when the experiments were begun.

Exp. 1. Small flat-bottomed glass dishes with sloping sides and an internal diameter on the bottom of about 4 cm. were used. About 12 c.c. of sea water were poured into each and, except in the two clean controls, the bottom was completely covered with sand or mud to a depth of 1 or 2 mm. Two dishes contained Salstone mud, one clean well-washed sand, and one, *E*, finer sand slightly overgrown with diatoms and therefore somewhat slimy. Twenty swimming larvae were put into each dish.

Table I indicates the results; it will be seen that the larvae rapidly disappeared in the dishes containing mud or sand while still swimming in the clean controls. The fine flocculent mud that formed a smooth surface layer in mud dishes B^1 and B^2 was on the second day marked with several tiny holes where the larvae may have crawled into it. In each dish on that day two larvae were observed on the mud surface; they were in what I have called the "sticky stage". A few similar ones were seen on the surface of the sand in dish *D*, where the majority were still swimming freely. An attempt was made to find those which had disappeared, but it proved a hopeless task in view of the relatively large quantity of mud and sand present. Another search 2 days later also failed to reveal any of them. In the light of further experience it can, however, be said that it is extremely probable that they were alive in the soils and undergoing metamorphosis.

On the third day three much smaller dishes were prepared and five larvae from clean control A^1 put into each. One of these dishes contained a little mud, one a little sand, and the third was left clean. By the next day the development of the larvae in the mud and sand dishes showed a definite advance over those in the controls.

TABLE I

(Exp. 1. Fertilization on May 2 1935)

Date	A^1 Control				A^2 Control				B^1 Mud			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
7. v. 35	20	.	.	.	20	.	.	.	20	.	.	.
8. v. 35	20	.	.	.	19	1	.	.	.	2	.	.
9. v. 35	20	.	.	.	18	2	.	.	0*	.	.	.
10. v. 35	See below				←18→		2	.	0	.	.	.

Date	B^2 Mud				D Cl. sand				E F. sand			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
7. v. 35	20	.	.	.	20	.	.	.	20	.	.	.
8. v. 35	.	2	.	.	*M*	*F**	.	.	*F*	.	.	.
9. v. 35	0*	.	.	.	5*	.	.	.	0*	.	.	.
10. v. 35	0	.	.	.	1	.	.	.	0	.	.	.

Subsidiary experiment with larvae from control A^1

Date	A^1 Control				Clean				Mud				Sand			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
9. v. 35	5	.	.	.	5	.	.	.	5	.	.	.	5	.	.	.
10. v. 35	←5→		.	.	4	1	.	.	.	.	2	3	1	.	1	2

Explanation of the Symbols used in the Tables

a, swimming larvae.
b, larvae in "sticky stage".
c, metamorphosing larvae.
d, young worms after metamorphosis.
F, few.
M, majority.
N, a fairly large number less than a majority.

All larvae found are recorded. An asterisk denotes that the dish was examined to determine the number of larvae swimming and whether any were visible on the surface of the soil, but that the soil itself was not searched. If the dish was not examined at all a dot appears in all four columns.

Exp. 2. This ran concurrently with Exp. 1. Smaller flat-bottomed glass dishes with vertical sides and an internal diameter of about 3 cm. were used. Each contained about 8 c.c. of sea water, and less soil than in the preceding experiment. Two additional soils were employed, one of clean coarse gravel and one of very fine flocculent mud. As before twenty swimming larvae were placed in each dish.

An examination of the results summarized in Table II shows definitely that by the third day larvae in the dishes containing bottom soils were on the whole advanced in development over those in the clean controls. This is clearly seen if the records on May 9 for thorough searches of the fine sand dish *E* and the mud dish B^1 be compared with those of controls A^1 and A^2. Unfortunately there was too much soil to make a thorough search of all the dishes practicable, but the results that were obtained from short searches of the clean sand *D* and flocculent mud *F* are, as far as they go, confirmatory evidence.

TABLE II

(Exp. 2. Fertilization on May 2 1935)

Date	A^1 Control				A^2 Control				B^1 Mud				B^2 Mud			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
7. v. 35	20	.	.	.	20	.	.	.	20	.	.	.	20	.	.	.
8. v. 35	19	1	.	.	18	2	.	.	1	.	.	.	.	1*	.	.
9. v. 35	14	6	.	.	15	3	2	.	.	3	11†	1	0*	.	.	.
10. v. 35	*F*	*M*	.	.	.	*M*	*F*	.	0*	.	.	.	0*	.	.	.

Date	*C* Gravel				*D* Cl. sand				*E* F. sand				*F* Fl. mud			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
7. v. 35	20	.	.	.	20	.	.	.	20	.	.	.	20	.	.	.
8. v. 35	*F*	.	.	.	*F*	.	.	.	*F*	.	.	.	.	2*	.	.
9. v. 35	.	.	1	1	.	1	.	6	3	.	1	11	.	1	1	5
10. v. 35	.	.	.	7	.	.	1*	.	0*	.	.	.	0*	.	.	.

† Eight of these had almost completed metamorphosis.

The preceding experiments having suggested that there does exist, in this species, a relation between metamorphosis and the substratum, it was decided that it would be worth while obtaining further data. Accordingly another fertilization was made on May 20 1935 and the following experiments performed. They were begun 3 days after fertilization instead of 5. The larvae were then at the stage shown in pl. I, fig. 2 of my 1933 paper, definitely earlier in development than those used in the first two experiments.

Exp. 3. The dishes used were the same as those in Exp. 1. Rather less soil was put into them, but the quantity was still relatively large. The fine and not very clean sand of dish *E* was omitted, otherwise the soils were of the same grades as before, although newly washed quantities were used. Fifty swimming larvae were put into each dish.

The amounts of soil were too large to search properly. It had been hoped that the bigger number of larvae would result in a few, at least, being found quickly, but this was not so. However, the experiment shows on the whole a quick descent into the mud and later into the sand, while a careful search of the sand in dish *D* on May 29 revealed that over half the worms, in fact all those found, had metamorphosed, while considerably fewer than half had metamorphosed in the controls. A search of a little of the mud in dish B^1, on the previous day, had yielded two metamorphosed worms at a time when none had metamorphosed in the controls. Doubtless other metamorphosed ones were present in the larger portion of the mud which was not searched thoroughly. Incidentally it may be mentioned that as late as September 4 three well-grown young worms were found in this dish.

The result on the gravel is a little difficult to interpret. The particles were so large that the larvae could swim freely in the interstices—as they were observed to do in the 1937 experiments—and some of them probably did this during the first three or four days of the experiment. At the time a note was made suggesting the possibility. Later one metamorphosed worm was seen crawling on the side of the dish but the fate of the other larvae is not known.

TABLE III

(Exp. 3. Fertilization on May 20 1935)

Date	*A*¹ Control				*A*² Control				*B*¹ Mud			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
23. v. 35	50	.	.	.	50	.	.	.	50	.	.	.
24. v. 35	50	.	.	.	50	.	.	.	4*	.	.	.
25. v. 35	50	.	.	.	50	.	.	.	3*	.	.	.
26. v. 35	50	.	.	.	50	.	.	.	1*	.	.	.
27. v. 35	48	2	.	.	48	2	.	.	.	.	1	1*
28. v. 35	*M*	*F*	.	.	*M*	*F*	.	.	.	1	.	2
29. v. 35	*F*	*M*	←12→		*F*	*M*	←*F*→		.	.	.	.
30. v. 35	2	.	*M*	*F*	3	.	*M*	*F*	.	.	.	.

Date	*B*² Mud				*C* Gravel				*D* Sand			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
23. v. 35	50	.	.	.	50	.	.	.	50	.	.	.
24. v. 35	12*	.	.	.	44*	.	.	.	47*	.	.	.
25. v. 35	12	1*	.	.	26*	.	.	.	29*	.	.	.
26. v. 35	14*	.	.	.	*N**	.	.	.	7*	.	.	.
27. v. 35	0*	.	.	.	9	.	.	1*	2	1*	.	.
28. v. 35	0*	.	.	.	0*	.	.	.	0*	.	.	.
29. v. 35	.	.	.	.	.	.	.	.	.	.	.	26
30. v. 35	.	.	.	.	.	.	.	.	.	.	.	.

Exp. 4. The small dishes of Exp. 2 were employed here. The control and mud dishes were not duplicated and less soil was used than before; it was thus possible to search more thoroughly, although as the experiment ran concurrently with Exps. 3 and 5 all the time could not be spent on it.

This experiment gave a very definite result. There was still too much mud to be satisfactory, but a search of the sand dish *D* yielded, on May 27, ten fully metamorphosed worms at a time when in the control none had properly started and all but two were still swimming freely. The count made 2 days later should also be noted. The relatively quick disappearance of swimming larvae in the mud dish is again seen.

TABLE IV

(Exp. 4. Fertilization on May 20 1935)

Date	*A* Control				*B* Mud				*C* Gravel				*D* Sand			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
23. v. 35	20	.	.	.	20	.	.	.	20	.	.	.	20	.	.	.
24. v. 35	20	.	.	.	6	2	.	.	20	.	.	.	20	.	.	.
25. v. 35	20	.	.	.	6*	.	.	.	15*	.	.	.	19*	.	.	.
26. v. 35	20	.	.	.	6*	.	.	.	*N**	.	.	.	7*	.	.	.
27. v. 35	18	2	.	.	.	1	.	.	7*	.	.	.	1	.	.	10
28. v. 35	*M*	*F*	.	.	.	.	1	1	1*	.	.	.	0*	.	.	.
29. v. 35	14	3	3	.	.	.	.	.	.	.	.	.	.	1	.	13

Exp. 5. This was a duplication of Exp. 4 with the exception that it was kept in the dark. It ran concurrently. If Table V, recording the results, be compared with Table IV, one striking difference will be noticed. In the present series the majority of the larvae in the mud dish continued to swim freely for some days longer than they did in Exp. 4, although for not so long as in the control, where incidentally most of the larvae metamorphosed a little sooner than in the corresponding control of Exp. 4. On other points the experiment is inconclusive, lack of time prevented thorough searches being made.

This apparent difference in behaviour between larvae kept in the light and others kept in the dark immediately led to the setting up of the following experiment designed to test this behaviour.

TABLE V

(Exp. 5. Fertilization on May 20 1935)

Date	*A* Control				*B* Mud				*C* Gravel				*D* Sand			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
23. v. 35	20	.	.	.	20	.	.	.	20	.	.	.	20	.	.	.
24. v. 35	20	.	.	.	17*	.	.	.	20	.	.	.	20	.	.	.
25. v. 35	20	.	.	.	16*	.	.	.	19*	.	.	.	20	.	.	.
26. v. 35	18	2	.	.	11*	.	.	.	F*	.	.	.	7	2*	.	.
27. v. 35	16	2	1	1	4*	.	.	.	3*	.	.	.	0*	.	.	.
29. v. 35	.	.	*F*	*M*	0*	.	.	.	0*	.	.	.	0*	.	.	.
1. vi. 35	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	.

Exp. 6. Two dishes, both containing mud, were prepared and thirty swimming larvae put into each; one was kept in the dark and the other placed alongside the dishes of Exp. 4. Table VI records the result: no significant difference was observed between the two lots of larvae; on the other hand, the majority of both continued to swim 1 day longer than those in the mud dish of Exp. 4, but for not quite so long as those in the mud dish of Exp. 5. Perhaps these small variations in behaviour as well as the greater contrast between Exps. 4 and 5 are only a degree more striking than the difference that occurred between the mud dishes B^1 and B^2 of Exp. 3. It will be remembered that all these larvae were from the same original culture.

TABLE VI

(Exp. 6. Fertilization on May 20 1935)

Date	In light				In dark				Date	In light				In dark			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*		*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
24. v. 35	30	.	.	.	30	.	.	.	27. v. 35	0*	.	.	.	0*	.	.	.
25. v. 35	19*	.	.	.	16*	.	.	.	29. v. 35	0*	.	.	.	0*	.	.	.
26. v. 35	7*	.	.	.	5*	.	.	.	31. v. 35	.	.	.	17	.	.	.	.

While the foregoing experiments indicated in a general way that larvae of *Notomastus* metamorphose earlier when in contact with a suitable bottom soil than when retained in clean glass vessels, they were not, in my opinion, entirely satisfactory. A sufficiently high proportion of metamorphosed worms had not been found, particularly in the mud dishes, and it was felt that, in order to show conclusively that the larvae had not merely been entrapped, smothered and killed in the mud, it would be necessary to demonstrate the presence alive of at least the majority of the young worms after metamorphosis. Accordingly it was decided to repeat the experiments and in the light of experience to improve the technique. The opportunity occurred in May 1937. In these later experiments less mud, sand, and gravel was used in each dish and this, together with superior optical equipment for conducting the search, yielded much better results.

On May 10 1937 mature *Notomastus* were obtained at Salcombe and a fertilization was made in Plymouth the same evening. On the following day most of the larvae were put into a plunger-jar, but some hundreds were kept in a clean finger-bowl. On May 14 the following two experiments (7 and 8) were begun, using larvae from the plunger-jar.

Exp. 7. Small glass dishes similar to those used in Exp. 2 were employed here. Only a little sand or mud, barely sufficient to cover the bottom in a very thin layer when evenly spread out, was introduced; it was, however, heaped around the sides, leaving some of the glass of the bottom exposed. On the second day a dish, B^3, containing a still smaller quantity of mud was added. In this instance the amount was too small to stay in a heap, it spread out and nowhere was there depth sufficient for a larva to bury itself. Twenty swimming larvae were put into each dish. The results are recorded in Table VII.

On May 17, the fourth day of the experiment, the first noteworthy result was obtained, although on the preceding two days there had been definite indications. In the clean sand dish *D* eleven metamorphosed worms were found together with one undergoing metamorphosis; none was swimming. In the clean controls all were swimming freely except one larva which was very lightly stuck by its tail end to the bottom; when released with a gentle squirt of water it swam at once. Next day a search of the mud dish B^2 recovered from the mud fourteen metamorphosed worms and two metamorphosing. In the controls the great majority were still actively swimming, and the few that were lightly stuck to the bottom had not begun to metamorphose but swam like the others when gently disturbed with a pipette. The evidence on this day, May 18, is quite conclusive, the majority of the larvae in mud dish B^2 and sand dish *D* had metamorphosed, while those of the same age in the controls had not begun. During succeeding days metamorphosis in the controls was very slow, so that even as late as May 20 when mud dish B^1 was searched the lag in their development was striking. Moreover, the worms in the controls were not as healthy as those in the soils.

The result in dish B^3 with very little mud was most interesting. The delay in metamorphosis during the first few days was almost as great as in the clean controls, but the larvae finally metamorphosed normally and were in excellent health on May 24 when those in the controls were showing signs of failing.

The larvae in the clean gravel dish *C* followed, in general, the course taken by those in the controls. The majority continued to swim for several days, often in the interstices among the heaped gravel fragments. When they did finally metamorphose they gradually became unhealthy.

Exp. 8. The dishes in this experiment were glass funnels of maximum diameter of about 8 cm. After careful cleaning the stems were blocked with a filling of paraffin wax and the funnels were then soaked in distilled water followed by sea water. They were supported in glass jars whose mouths were a little smaller in diameter than those of the funnels; the greater part of each funnel was thus inside its jar. Black paper was tied around the latter to ensure that the funnel would be lit only from above, as the sea bottom is illuminated in nature. Each funnel was partially filled with about 30 c.c. of filtered sea water and covered with a glass plate to keep out the dust. A sheet of white paper laid on top cut off the main strength of the light.

Funnels were chosen because they enabled a relatively large volume of water to be used in conjunction with very little bottom soil, for the latter would sink into the apex at the bottom, where larvae would also tend to collect whenever they swam downwards. On the whole the device was very satisfactory.

As usual two clean controls and two mud vessels were included together with one containing clean sand and one clean gravel. Twenty larvae were put into each and the experiment ran concurrently with Exp. 7, and as in this a third mud vessel with a very small quantity of mud was added on the second day.

On account of their shape the funnels were more difficult to examine than the glass dishes; they were not at all easy to search with the binocular microscope, and a simple hand-lens gave too low a magnification to be really useful. Hence even in the clean controls larvae were occasionally missed. Although the figures are not quite so complete as for Exp. 7 the result is none the less definite. An early descent into the mud was clearly indicated, and a little later into the sand. From a study of Table VIII it is obvious too that metamorphosis took place sooner in the mud and sand than in the gravel or the controls. Again, too, the health of those in all three mud vessels and in the sand was much better on May 27 and 28 than was that of the worms in the controls and in the gravel. These latter were in poor condition.

Mud vessel B^3 was extremely interesting in comparison with the similar dish in Exp. 7; the larvae stopped swimming almost as rapidly as in the funnels with much more mud. The reason appears to be that whereas in Exp. 7 the very small quantity of mud was scattered thinly over a wide area, in the present experiment the same quantity was gathered together in a small depression in the middle of the wax plug and the larvae could bury themselves in it.

Exp. 9. This was designed to test the results obtained with vessels B^3 of Exps. 7 and 8, where it seemed that a very little mud would have less effect

TABLE VII

(Exp. 7. Fertilization on May 10 1937)

Date	A^1 Control				A^2 Control				B^1 Mud				B^2 Mud				B^3 Little mud				C Gravel				D Sand			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
14. v. 37	20	.	.	.	20	.	.	.	20	.	.	.	20	.	.	.					20	.	.	.	20	.	.	.
15. v. 37	20	.	.	.	20	.	.	.	13	1	.	.	12	2	.	.	20	.	.	.	20	.	.	.	5	13	.	.
16. v. 37	19	1	.	.	20	.	.	.	0*	.	.	.	1	1	1	1	17	2	.	.	20	.	.	.	2	11	4	.
17. v. 37	20	.	.	.	19	1	.	.	0*	.	.	.	1*	.	.	.	18	1	1	.	19	.	.	.	.	1	1	11
18. v. 37	19†	1	.	.	16	4	.	.	0*	.	.	.	.	1	2	14	14	1	.	3	17	.	.	.	.	.	.	11‡
19. v. 37	3	4	1	.	16	1	3	.	0*	.	.	.	1*	.	.	.	8	1*	.	.	11	2	.	.	0*	.	.	.
20. v. 37	.	6	1	1	5	6	4	5	.	.	.	15	0*	.	.	.	4*	.	.	.	6	4	1*	.	0*	.	.	.
21. v. 37	.	.	5	3	2	7	4	7	0*	.	.	.	0*	.	.	.	0*	.	.	.	.	4	1	.	.	.	.	2
22. v. 37	Unhealthy				4	←	16	→	.	.	.	.	.	.	.	.	0*	.	.	.	0*	.	.	.	.	.	.	.
24. v. 37	Dead and dying				1	.	.	19	.	.	.	.	.	.	.	.	.	.	.	17	Unhealthy				.	.	.	.
26. v. 37	Dead				Unhealthy				.	.	.	14	.	.	.	13	.	.	.	.	.	.	4	8	.	.	.	.
																					(six dead)							

† 12 larvae preserved. ‡ 11 worms preserved.

TABLE VIII

(Exp. 8. Fertilization May 10 1937)

Date	A^1 Control				A^2 Control				B^1 Mud				B^2 Mud				B^3 Little mud				C Gravel				D Sand			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
14. v. 37	20	.	.	.	20	.	.	.	20	.	.	.	20	.	.	.					20	.	.	.	20	.	.	.
15. v. 37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.	.	.
16. v. 37	19	.	.	.	20	.	.	.	0*	.	.	.	0*	.	.	.	2	8	6	.	*M**	.	.	.	16	2	2	.
17. v. 37	18	.	.	.	19	.	.	.	0*	.	.	.	0*	.	.	.	.	5	6	3	13	.	.	.	1	10	4	5
18. v. 37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
19. v. 37	13	4	.	.	14	4	.	.	0*	.	.	.	.	.	.	17	.	1	.	13	10	2	1	.	0*	.	.	.
20. v. 37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
21. v. 37	.	14	.	.	2	*M*	.	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27. v. 37	.	1	6	4	.	.	9	6	.	.	.	.	.	.	.	.	.	.	.	11	.	.	4	9	.	.	.	16
	(mainly unhealthy)				(mainly unhealthy)																(mainly unhealthy)							
28. v. 37	.	.	.	.	.	.	.	.	.	.	.	13	.	.	.	13	.	.	.	.	.	.	.	.	.	.	.	.

when spread out in a very thin layer. Three flat-bottomed glass dishes, 4·5 cm. in diameter, were partially filled with about 18 c.c. filtered sea water. One was a clean control, one contained a fairly large quantity of mud in heaps on the bottom, while the third had a very little mud scattered thinly so that it was nowhere deep enough for larvae to burrow. The results show that in the latter dish the majority of the larvae continued to swim for a longer period than in the dish with much mud.

TABLE IX

(Exp. 9. Fertilization on May 10 1937)

Date	Control				Much mud				Little mud			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
17. v. 37	20	.	.	.	20	.	.	.	20	.	.	.
18. v. 37	14	6	.	.	2*	.	.	.	14	2*	.	.
19. v. 37	16	4	.	.	1*	.	.	.	11	2*	.	.
20. v. 37	12	8	.	.	1*	.	.	.	5*	.	.	.
21. v. 37	10	10	.	.	0*	.	.	.	2	5*	.	.
22. v. 37	7	←13→		.	0*	.	.	.	0*	.	.	.
24. v. 37	*F*	← *M* →			.	.	.	.	.	.	.	.
	(some unhealthy)											
26. v. 37	(dead and dying)				.	.	.	.	.	.	.	.

Exp. 10. During the progress of the last three experiments a clean finger-bowl containing several hundreds of larvae from the same fertilization was kept on the bench alongside. Temperature conditions would be identical with those in the experimental dishes, but the bowl was nearer to the window (north) and received a little extra light. It is interesting to give the records for this bowl which was examined from time to time after the first few days. No counts were made, but rough proportions were easily estimated. These records (Table X) should be compared with the counts made on corresponding dates in Exps. 7, 8 and 9, because the finger-bowl can be regarded as a major clean control. It followed closely the course of the experimental controls with a tendency to slightly more advanced development, perhaps because of the greater crowding. These larvae were, however, definitely delayed in their development compared with those in the mud and sand dishes.

On May 20, about 4 days after the majority of the larvae provided with mud or sand had begun to metamorphose, it was decided to test some of the larvae still swimming freely in this finger-bowl. Accordingly twenty were picked out and placed in a dish containing mud. Most of them, if not all, metamorphosed. A count on May 28 gave seventeen worms, fifteen of them in excellent health, but two not so well, one being definitely abnormal. Three could not be found; it is possible they were missed but they might have been dead. Their deaths, however, would not alter the conclusion that the majority of the larvae can metamorphose normally several days after the time at which this first becomes possible and that their health is not adversely affected by the delay.

Exp. 11. This was a simple test to show what effect, if any, darkness would have on larvae kept in a clean control dish. On May 19 twenty swimming larvae from the finger-bowl were put into such a dish which was then kept in a light-tight box except for the few minutes whenever it was examined. The development of the larvae followed closely that of those in the other controls; there was, perhaps, a slight tendency to delay. This was not, however, sufficiently marked to be significant. It will be remembered that in Exp. 5 the tendency was in the opposite direction.

Table X

(Exp. 10. Fertilization on May 10 1937)

Date	Clean finger-bowl				Test mud			
11. v. 37	Several hundred stage *a*							
	a	*b*	*c*	*d*	*a*	*b*	*c*	*d*
17. v. 37	*ca.* 50 %	*ca.* 50 %	.	.				
19. v. 37	*ca.* 50 %	*ca.* 50 %	.	.				
20. v. 37	*ca.* $33\frac{1}{3}$ %	←*ca.* $66\frac{2}{3}$ %→		.	20	.	.	.
21. v. 37	*F*	←*M*→		*F*	.	.	.	.
22. v. 37	*F*	*F*	←*M*→		.	4	.	13
					(3 or 4 unhealthy)			
24. v. 37	.	←*F*→		*M*	.	.	.	.
26. v. 37	.	.	.	*M*	.	.	.	.
	(a few abnormal and a few dead)							
28. v. 37	.	.	.	.	.	.	.	17
					(two unhealthy)			
29. v. 37	(a few living, majority dead)				.	.	.	.

Table XI

(Exp. 11. Fertilization on May 10 1937)

Date	Clean dish in dark				Date	Clean dish in dark			
	a	*b*	*c*	*d*		*a*	*b*	*c*	*d*
19. v. 37	20	.	.	.	24. v. 37	*F*	.	*N*	*F*
20. v. 37	10	10	.	.	26. v. 37	.	.	.	20
22. v. 37	*M*	*F*	*F*	.		(unhealthy)			
					29. v. 37	(unhealthy and dead)			

Discussion of the Results

A consideration of the results leaves no doubt that *Notomastus* larvae will settle and metamorphose sooner when provided with mud or sand than when kept in perfectly clean glass vessels, other conditions being uniform. It seems fairly clear also that larvae will settle much more readily into mud or sand than into clean gravel, the latter being a soil in which the adults are not found. This is seen clearly in Exps. 7 and 8, and to some extent in 2, 3 and 4 where the gravel was probably not washed quite so clean as in the 1937 experiments. Exp. 5, however, is an exception to this, although the difference may be more apparent than real in that the gravel was not searched and that some of the larvae at any rate may have been swimming in the interstices. It will be remembered, too, that in this experiment the swimming of the larvae in the mud dish was unduly prolonged.

The adults are found much more commonly in soft mud than in sand. It was thought that a distinct preference for the former would be shown, but the results are not very definite on this point. Exps. 1, 2, 4 and 8—and on the whole 3—seem to show such a preference, but Exps. 7 and 5 taken alone would indicate a liking for sand before mud, although it will be admitted that this preference is not at all strongly shown, and Exp. 5 is in any case an exception to the series in some respects. Taking all the experiments into consideration it may perhaps be said that larvae will generally settle a little more quickly into mud than into sand, but that the difference in effect between the two soils is not at all great.

Growth of the young worms between metamorphosis and the stage at which they normally begin to feed was generally much better in the mud and sand vessels than in the clean controls, where they usually soon became unhealthy and died. The same thing happened as a rule in the clean gravel where events on the whole followed closely the sequence of the controls. In mud or sand worms would be in excellent health several days after metamorphosis. In these soils also absorption of the yolk was in advance of that in the controls; thus in Exp. 8 it was nearly all absorbed by May 27 and 28 in the worms living in sand or mud, whereas the not very healthy worms in the controls had a fair quantity left. Moreover, the former had by that time six chaetigers, while the control worms had only five. In the mud the worms were on those dates beginning to swallow debris, although in the sand they were eating little or nothing, probably because the fragments were too large and no organic debris was present.

With the Mitraria larva of *Owenia* it was discovered (Wilson, 1932) that a mere sprinkling of sand grains was sufficient to bring about metamorphosis, although the time taken to begin this after supplying the grains was much longer than when a fairly thick layer was given. Similarly for *Notomastus*, Exps. 7 and 9 have shown that a slight sprinkling of mud is effective in producing metamorphosis in advance of the clean controls, but at a longer interval of time than when the mud lies thickly. Exp. 8 shows, so it would seem, that it is only necessary for the mud to be deep enough for the larvae to bury themselves; the total quantity may be very small indeed. After metamorphosis the worms live as healthily as do those in thicker mud, even when it is very thinly scattered as it was in dish B^3 of Exp. 7.

The influence, if any, of light is not at all clear. The experiments give hopelessly inadequate and contradictory data on this point; only further work can show whether light has any influence at all.

Further experiments might also be done to find out the effect of artificial soils of various substances and of differing grades. This perhaps would establish whether the effect is caused merely by particle size or whether there is in natural muds and sands, even after boiling, something of a more subtle and at present indefinable nature.

We have seen definitely that larvae provided with mud or sand metamorphose earlier than do those without it. Exp. 10 has shown also that larvae which have been swimming in a clean vessel for some days longer than they would have done had a suitable bottom soil been available, will metamorphose if given such a soil and will continue normal healthy development. Thus there is in the larval life of this species a period of 2 or 3 days at least during which it can at any time settle and metamorphose. Under natural conditions this must be of very great value to the larvae when they are drifted along by tidal and other currents and come into contact with bottom soils of varying grade. It is possible for them to enter a soil and if it be not suitable to come out again. In the *Notomastus* experiments this often happened; it was also observed with *Scolecolepis* (Day & Wilson, 1934). The larvae are likely to be in the bottom layers during the last free-swimming stage; at any rate in the plunger-jars and finger-bowls they then keep down close to the bottom, in contrast with the earlier stages which crowd up to the surface.

If a selective power on the part of larvae and an ability to metamorphose at any time during a fairly long period were eventually found to be general for bottom-living forms—especially those sharply restricted as to the nature of the soil in which they live—we should have advanced in our understanding of the means by which species are distributed. There would, it is true, remain other aspects of the problem to be taken into consideration. *Scolecolepis* larvae, for instance, select mud, but how do they find their right level on the shore? To that extent, perhaps, their settling may be pure chance, unless it happens that they are most strongly attracted to mud inhabited by the adults. We may be sure, however, that a power of selection would not eliminate all risks, shore forms would still be in danger of being swept out to deep water and lost, while larvae might never be drifted over the right kind of soil. Nevertheless, it would lessen very materially the dangers inherent in the possession of pelagic larvae, and the wastage in reproduction.

Summary

The question is raised how pelagic larvae of marine bottom animals reach a type of substratum suitable for adult life. Attention is drawn to a few forms in which it is not entirely due to chance, since their larvae have been shown to exercise some degree of choice of the soil on which they will settle, and to be capable of preserving the ability to metamorphose for several days at least. These powers, if found to be fairly general in marine bottom animals, would have important bearings on distribution problems. There is supporting evidence from the investigations of *Notomastus latericeus* Sars here described. The adult is found in mud or muddy sand. Experiments showed that larvae of this species if provided with mud or sand generally metamorphose several days before those kept in clean glass vessels or with clean shell gravel. Mud perhaps induces slightly more rapid settling than sand. After metamorphosis the growth and health of the young worms is generally much better in mud or sand than in gravel or clean glass vessels.

REFERENCES

Davis, F. M., 1923. Quantitative studies on the fauna of the sea bottom. No. 1. Preliminary investigation of the Dogger Bank. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. VI, No. 2, pp. 1–54.

Day, J. H. & Wilson, D. P., 1934. On the relation of the substratum to the metamorphosis of *Scolecolepis fuliginosa* (Claparède). *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 655–62.

Grave, G. & Woodbridge, H., 1924. *Botryllus schlosseri* (Pallas): The behaviour and morphology of the free-swimming larva. *Journ. Morph.*, Vol. 39, pp. 207–47.

Lebour, M. V., 1931. The larval stages of *Nassarius reticulatus* and *Nassarius incrassatus*. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 797–818.

—— 1933. The larval stages of *Erato voluta* (Montagu). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 485–90.

—— 1933. The eggs and larvae of *Philbertia gracilis* (Montagu). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 507–10.

—— 1934. Rissoid larvae as food of the young herring. The eggs and larvae of the Plymouth Rissoidae. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 523–39.

—— 1934. The eggs and larvae of some British Turridae. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 541–54.

—— 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 547–65.

Prytherch, H. F., 1934. The role of copper in the setting, metamorphosis, and distribution of the American oyster, *Ostrea virginica*. *Ecological Monographs*, Vol. 4, pp. 47–107.

Visscher, J. P., 1928. Reactions of the cyprid larvae of barnacles at the time of attachment. *Biol. Bull.*, Vol. LIV, pp. 327–35.

Visscher, J. P. & Luce, R. H., 1928. Reactions of the cyprid larvae of barnacles to light with special reference to spectral colors. *Biol. Bull.*, Vol. LIV, pp. 336–50.

Wilson, D. P., 1932. On the Mitraria larva of *Owenia fusiformis* Delle Chiaje. *Phil. Trans. Roy. Soc.*, Ser. B, Vol. 221, pp. 231–334.

—— 1933. The larval stages of *Notomastus latericeus* Sars. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 511–18.

—— 1936. The development of the sabellid *Branchiomma vesiculosum*. *Quart. Journ. Micro. Sci.*, Vol. 78, pp. 543–603.

Yonge, C. M., 1937. The biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.). *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 687–703.

ON THE GROWTH AND FEEDING OF THE LARVAL AND POST-LARVAL STAGES OF THE CLYDE HERRING

By S. M. Marshall, D.Sc., A. G. Nicholls, Ph.D. and
A. P. Orr, M.A., D.Sc.

Marine Station, Millport

(Text-figs. 1–4)

CONTENTS

	PAGE
Introduction	245
Collection of Material	245
Size and Growth	248
Food and its Relation to the Plankton	252
Weight and Composition	260
Experimental Work	263
Summary	266
References	267

INTRODUCTION

The comparatively enclosed waters of the Clyde sea-area offer an opportunity of studying the biology of herring larvae from one spawning area.

The chief spawning here takes place in spring and there are two well known grounds, one on the Ballantrae Banks off the coast of south Ayrshire, and the second on the Iron Rock Ledges off the south-west coast of Arran (Fig. 1). These grounds have long been known to Clyde fishermen, and "spawny" haddock have been recorded from both places by Clark (1933).

It was decided to follow the development of the eggs spawned on the Iron Rock Ledges because they are in a more sheltered position and are more accessible from the laboratory than the Ballantrae Banks. The intention was to take weekly samples of the larvae and to follow the changes in length, weight, chemical composition, and food and to correlate the last with changes in the plankton.

COLLECTION OF MATERIAL

Spawning usually takes place towards the end of February or early in March, and several attempts were made about that time to find the spawn by dredging. On March 19 1934 spawn was obtained on small boulders, pebbles and *Laminaria* at the Iron Rock Ledges. On the same date a few larvae, chiefly at the yolk-sac stage, were caught by townetting; thereafter the

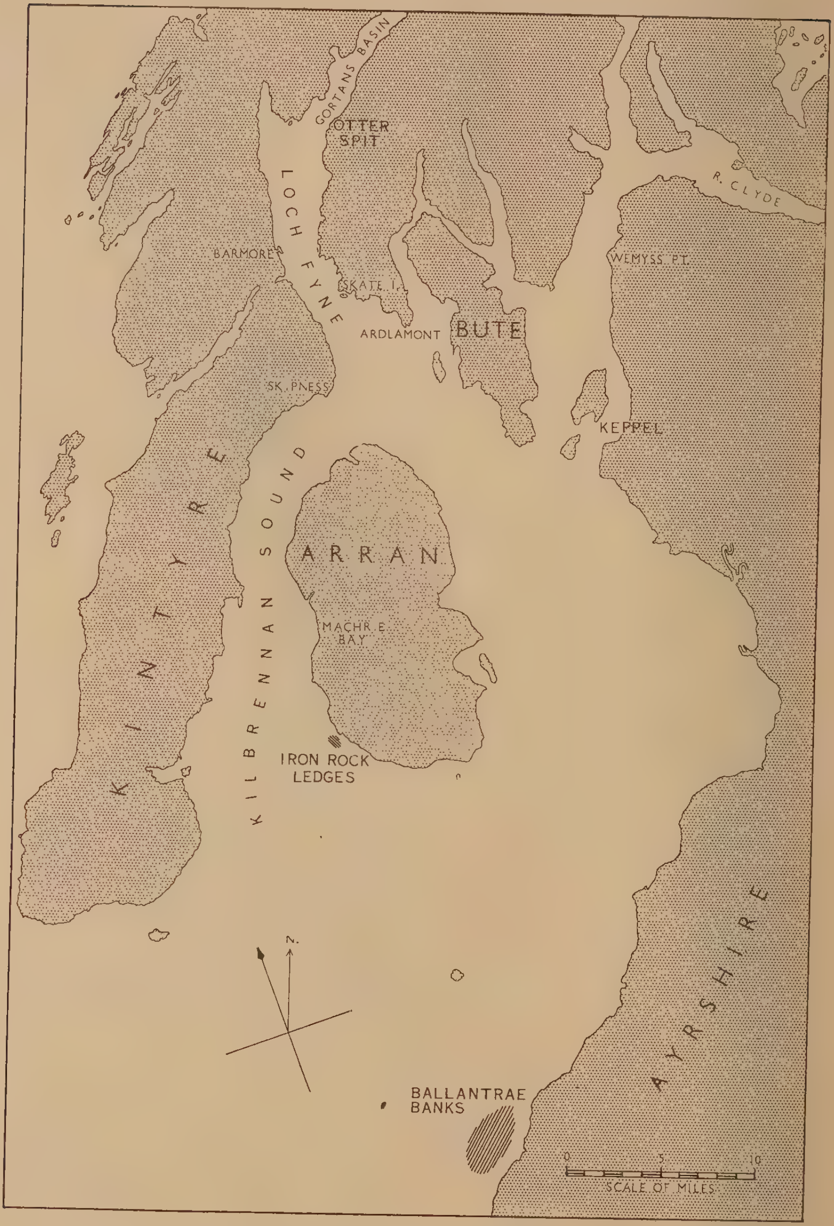

GORTANS BASIN
OTTER SPIT
LOCH FYNE
BARMORE
SKATE I.
ARDLAMONT
BUTE
R. CLYDE
WEMYSS PT.
KEPPEL
SK. PNESS
KILBRENNAN SOUND
ARRAN
MACHRIE BAY
IRON ROCK LEDGES
KINTYRE
N.
BALLANTRAE BANKS
AYRSHIRE
0
5
10
SCALE OF MILES

Fig. 1. The Clyde sea-area, showing localities where young herring were found. Spawning grounds hatched.

gradually developing larvae were captured at intervals of about a week until April 30. They appeared to move northwards, for after the first week or two more were caught in Machrie Bay, about 6 miles to the north, than at the Iron Rock Ledges. During and after April ctenophores and medusae became unusually abundant and killed the few larvae caught in the townettings. No herring were caught after April 30 in spite of an intensive search, and it is possible that the abundance of ctenophores and medusae was, at least in part, responsible for this. It is also possible, however, that had townettings been taken at night, as in the following year, they would have been more successful.

Larvae were obtained for a few days in townettings off Keppel Pier at the end of April and beginning of May, but these also disappeared.

Owing to the failure to obtain herring later than April in 1934 an effort was made the following year to complete the series up to metamorphosis. In 1935 larvae were found on April 2. The catch consisted mainly of yolk-sac stages but, as might be expected from the slightly later date, there were also larger specimens up to 13 mm. In the two following weeks larvae were taken in Machrie Bay, but in diminishing numbers, and by April 16 they had almost disappeared, just as in the previous year. In view of Russell's (1930) finding that larval clupeids were more readily obtained in the dark, hauls were taken the following week at night in the Kilbrennan Sound and the mouth of Loch Fyne and good catches were obtained off Skipness and Barmore Peninsula. The herring were therefore still moving north. Night hauls (between dusk and dawn) were continued and weekly samples taken until the beginning of June. During this time most were obtained at a position just south of the Otter Spit in Loch Fyne. This represents the limit of the northward migration for, although frequent hauls were taken in the Gortans Basin to the north of this, only a few herring were caught.

As in 1934 herring larvae were caught off Keppel Pier in large numbers at the end of April and beginning of May and these were later followed north and caught off Wemyss Point. Thus while the herring from the Iron Rock Ledges migrated in a northerly direction up the Kilbrennan Sound and reached the lower part of Loch Fyne, where they stayed till metamorphosis, it seems probable that the herring taken off Keppel Pier and Wemyss Point originated on the Ballantrae Banks and migrated in a similar direction along the east coast of the Firth of Clyde.

Until May 27 the net used was a two metre stramin adapted to a rectangular frame, but on this date the catches were very small and three days later a Poole Sprat Trawl with a stramin cod-end was used instead and proved successful. On June 5, however, the catch even with this net was very small and a few of the herring were metamorphosing. From this time onwards, apart from an occasional metamorphosed specimen, no herring were taken despite a thorough search, using the Poole Sprat Trawl in deep and shallow water and a fine-meshed shore seine in many of the sandy bays of the area.

The larvae over the spawning ground were taken in mid-water or near the bottom (15 m.) but may have been generally distributed. As they were followed northwards only hauls in deeper water (20–40 m.) were successful. These were daylight hauls and the larvae were soon lost. After night hauls were begun larvae were found near the surface, always above 5 m. until May 7, but as the time of metamorphosis approached they remained in deeper water. On May 14 the majority (about 1900 in a 15 min. haul) were taken at 10 m. whereas a surface haul produced under 20. On May 21 and 30 the largest catches were at 20 m., with very few either above or below. The few specimens obtained on June 5 were caught at various depths.

The results of the collections are summarized in Table I. Immediately on capture the herring, except those for chemical analysis, were fixed in 5% neutral formalin.

SIZE AND GROWTH

Our own observations, supplemented by the reports of the Fishery Officers of the Clyde District, enable us to fix with a certain degree of accuracy the date of hatching of the larvae. In 1934, although some spawning was reported by the Fishery Officers as early as February 17, the main spawning appears to have occurred at the Iron Rock Ledges during the week ending March 10. Spawn was dredged on March 19 and brought into the laboratory where at a temperature of about 7° C. it was hatching by March 23. There were thus from 13 to 20 days between spawning and hatching. In the laboratory further samples of herring spawn had been artificially fertilized and at tank temperatures of about 7° C. took about a fortnight to hatch. The temperature of the sea on the spawning ground at this time was only slightly if at all lower (March 13, 7·2° C.; March 19, 6·88° C.), so that the period of development may be assumed to be between a fortnight and three weeks. Thus with spawning in the sea taking place between March 3 and 10, hatching may be assumed to have taken place chiefly between March 16 and 23.

The observations of Meyer (quoted by Williamson, 1910) and Williamson (1910, 1911) on the influence of temperature on the time of hatching of herring ova were made at temperatures either below or (in one case) above these. So far as our results can be compared with theirs they are in agreement.

In 1935 the Fishery Officers reported herring "mazy" at the Iron Rock Ledges during the week ending March 2 and "running" during the week ending March 9. Thus the date in 1935 is within a day or two of that in 1934 and sufficiently close for the 2 years' results to be considered together. It was impossible to confirm this date in 1935 as no hauls could be taken until April 2. It is assumed that the larvae caught on March 19 1934 were just hatched and that date has been taken as the zero point in both years on which to base the approximate age in days of the fish caught, as shown in Table I.

On each occasion that herring were taken, either the whole catch or a sample of it was measured. The results are shown in Table II and the median lengths are shown in Table I and Fig. 2. Measurements were made from the tip of the snout to the end of the tail, or to the tip of the dorsal fluke after that had developed. At the time of hatching the larvae measured about 7 mm. and from then until metamorphosis, as shown by Fig. 2, there is a regular weekly increment of about 3 mm. The points do not lie on a straight line but it is obvious that, apart from four points, a straight line expresses the relationship best. It is believed that the catches belonging to these four points are not truly representative of the main shoal. The sample taken on April 2 1935, which has too low a value, was taken at the Iron Rock Ledges over the spawning ground, some time after hatching had begun and although a few large specimens were included the catch was composed mainly of late-hatching larvae. A similar explanation probably applies to the catch of April 30 1934, which was the last taken in Kilbrennan Sound that year. It was from Machrie Bay and probably represents larvae hatched later than the main mass which, judging from the 1935 results, had very probably moved farther north by this time. The

TABLE I. HERRING SAMPLES FROM CLYDE SEA-AREA, 1934–35

Date	Place	Approximate age in days after hatching	Approximate total catch		No. measured	Length in mm.	
						Median	Average
1934							
March 19	Iron Rock Ledges	3	200		53	7·8*	7·3*
,, 27	Iron Rock Ledges	11	400		83	8·2	7·6
April 2	Iron Rock Ledges	17	32		32	11·3	10·7
,, 9	Machrie Bay	24	70		69	14·8	12·8
,, 30	Machrie Bay	45	30		30	18·8	18·3
May 1	Keppel	46	300		104	21·6	21·1
1935							
April 3	Iron Rock Ledges	18	30		24	7·2	7·3
,, 9	Machrie Bay	24	61		61	14·7	14·2
,, 16	Machrie Bay	31	3		3	—	—
,, 22	Keppel	37	221		221	20·7	20·2
,, 23	Skipness Barmore	38	251 160	411	268	21·9	21·2
,, 29	Barmore Otter Spit	44	490 495	985	378	26·2	25·6
May 2	Wemyss Point	47	556		338	26·8	26·2
,, 7	Otter Spit Gortans Basin Ardlamont	52	824 11 128	963	441	27·3	26·4
,, 14	Otter Spit Ardlamont	59	2228 28	2256	461	32·6	31·6
,, 21	Otter Spit Ardlamont	66	1394 4	1398	239	35·2	34·0
,, 27	Skate I.	72	8		8	—	—
,, 30	Otter Spit	75	3114		265	36·9	36·4
June 5	Otter Spit	81	50		25	37·5	37·9
,, 17	Barmore	93	1		1	—	—

* The tails of the herring were not included in these measurements.

herring from Keppel on May 1 1934 were smaller than those taken at the same time in 1935 from Wemyss Point, which suggests either that the herring from

TABLE II. LENGTH MEASUREMENTS OF HERRING

	1934						1935										
	March		April			May	April					May					June
Mm.	19	27	2	9	30	1 Keppel	3	9	22 Keppel	23	29	2 Wemyss Pt.	7	14	21	30	5
6	7	9	—	—	—	—	11	—	—	—	—	—	—	—	—	—	—
7	24	26	—	—	—	—	7	—	—	—	—	—	—	—	—	—	—
8	21	40	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—
9	1	8	2	—	—	—	1	—	—	—	—	—	—	—	—	—	—
10	—	—	10	—	—	—	1	3	—	—	—	—	—	—	—	—	—
11	—	—	17	8	—	—	1	—	—	—	—	—	—	—	—	—	—
12	—	—	2	15	—	—	—	2	—	—	—	—	—	—	—	—	—
13	—	—	1	30	—	—	1	10	—	—	—	—	—	—	—	—	—
14	—	—	—	14	—	—	—	23	—	—	—	—	—	—	—	—	—
15	—	—	—	2	1	—	—	10	1	1	—	—	—		—	—	
16	—	—	—	—	4	—	—	10	1	—	—	—	—			—	—
17	—	—	—	—	1	—	—	3	7	5	—	—	—	—		—	—
18	—	—	—	—	12	7	—	—	18	5	—	—	—	—	—	—	
19	—	—	—	—	5	16	—	—	56	37	—	—	—	—	—	—	—
20	—	—	—	—	4	13	—	—	41	45	—	1	1	—	—	—	—
21	—	—	—	—	3	27	—	—	49	48	1	1	12	—	—	—	—
22	—	—	—	—	—	22	—	—	26	55	9	5	31	—	—	—	—
23	—	—	—	—	—	15	—	—	20	51	29	14	34	—	—	—	—
24	—	—	—	—	—	2	—	—	2	20	52	27	22	1	—	—	—
25	—	—	—	—	—	2	—	—	—	1	78	44	37	3	—	—	—
26	—	—	—	—	—	—	—	—	—	—	110	92	66	10	—	—	—
27	—	—	—		—	—	—	—		—	69	90	68	38	—	—	—
28	—	—	—	—	—	—	—	—	—	—	21	58	77	27	5	—	—
29	—	—	—	—	—	—	—	—	—	—	8	6	49	29	9	—	—
30	—	—	—	—	—	—	—	—	—	—	1	—	26	40	12	1	—
31	—	—	—	—	—	—	—	—	—	—	—	—	12	52	19	—	1
32	—	—	—	—	—	—	—	—	—	—		—	6	49	23	1	1
33	—	—	—	—	—	—	—	—	—	—	—	—	—	81	25	9	2
34	—	—	—	—	—	—	—	—	—	—	—	—	—	60	20	31	3
35	—	—	—	—	—	—	—	—	—	—	—	—	—	52	30	45	4
36	—	—	—	—	—	—	—	—	—	—	—	—	—	16	34	54	—
37	—	—	—	—	—	—	—	—	—	—	—	—	—	3	28	50	4
38	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	39	1
39	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	23	1
40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	6	1
41	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	1
42	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
43	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
44	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
46	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
47	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
49	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Total	53	83	32	69	30	104	24	61	221	268	378	338	441	461	239	265	25

Ballantrae Banks in 1934 were smaller than those of 1935, or more probably, that we were again dealing with late-hatching larvae, the main shoal being farther north. The second alternative is supported by the catch from Keppel on April 22 1935, which although of similar size to that of May 1 1934, was taken as much as nine days earlier. Moreover, both the 1935 catches of presumed Ballantrae origin fit in well with the main curve. The last haul (June 5 1935) was a poor sample (25 fish) and was taken at the time of metamorphosis when most of the herring had disappeared from our catches leaving only fish which would be late hatchers or poor growers and therefore smaller. The effect of the larger fish metamorphosing and disappearing would probably affect the previous haul (May 30) to a certain extent.

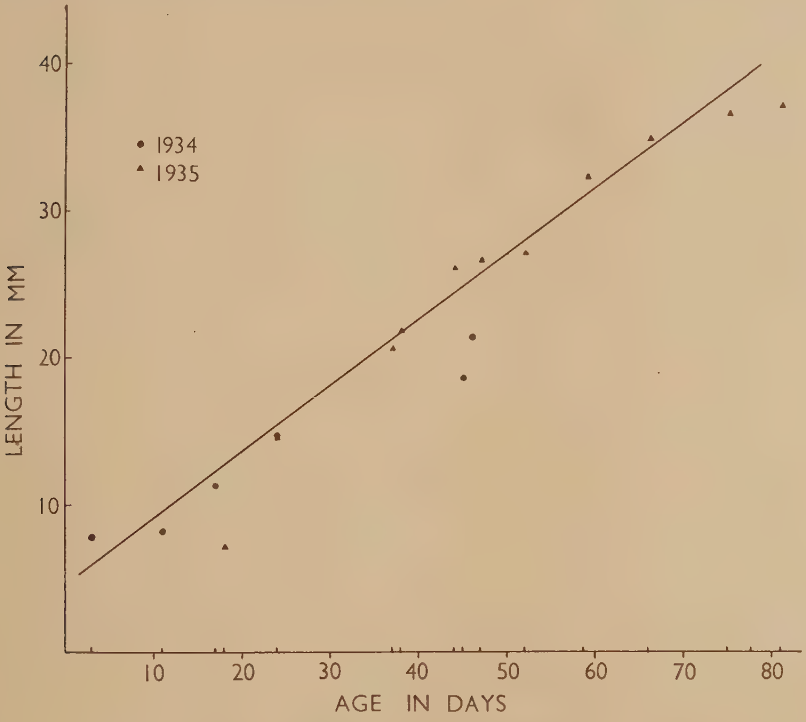


Fig. 2. Relation of length to age in pre-metamorphosis herring.

In the samples the range in size gradually increased as the larvae grew, owing in part at least to the unequal growth of the individuals.

A comparison of the rate of growth of the Clyde herring larvae with those from elsewhere shows on the whole a good agreement. Obviously the comparison can be made only with spring spawned herring because autumn spawned fish are exposed to different conditions of temperature and feeding. Meyer (1878), dealing with the spring Baltic herring spawned in March in Kiel Bay, concluded that the larvae reached a size of 17–18 mm. at 1 month, 34–36 mm. at 2 months, and 45–50 mm. at 3 months. The results of Ekstrom, Nilsson, and Hoek, summarized by Fulton (1906), and those of Runnstrøm (1934) also agree fairly well although the growth in their herring seems to slow off in May and June, so that metamorphosis does not take place until July or August. The only divergent results are those of Masterman (1896) on herring caught in St Andrews Bay. Although his larvae, hatched in mid-March, were 15 mm. at the end of 1 month, a figure which agrees fairly well with ours, the growth after this was only 4–5 mm. per month, so that after 7 months, the herring were only 44 mm. The results of the collections of larvae made by the Fishery Board for Scotland from 1904–32 (Clark, 1933) show, for the spring hatched larvae, a slow growth in the early months and a rapid growth in the later months. This is not borne out by our results, which show a uniform monthly increment, although the size attained in June is much the same in both cases.

The stage of development reached by the Clyde herring at any particular length agrees well with Lebour's (1921 *a*) description. Thus the larvae lose the yolk-sac and begin to develop the dorsal fin at about 10 mm., the end of the notochord turns up at about 17 mm. and pelvic fins appear at about 22 mm. When the Clyde larvae were about 30–35 mm. the caecal part of the stomach began to form and the air bladder became prominent. The smallest metamorphosing herring measured 42 mm.

FOOD AND ITS RELATION TO THE PLANKTON

Food

In every catch of herring larvae, the guts of those feeding were examined and their contents noted. The proportion feeding was seldom large and was sometimes as low as 1 %. Hardy (1924) has suggested that on capture the young herring ejects the food in the gut, and this is possibly the cause of the small proportion containing food. Quite often there were swellings in the empty gut as if it had recently contained food.

The food was almost invariably in the intestine, unless the fish had begun metamorphosis, and although crushed and often broken up the greater part was usually recognizable. Table III shows the food from all the guts examined in each day's catch, expressed as the numbers of organisms in 100 feeding herring. The identifications may not be invariably correct, especially where it depends on size, but most of the copepodites were easily recognizable.

It is well known (Lebour, 1921 *b*, 1924; Hardy, 1924; Ogilvie, 1927) that herring larvae feed first on diatoms and unicellular organisms. Although recognizable diatom skeletons were found in only a few of the present samples, there was in the guts of most of the yolk-sac stages which contained anything a greenish mush, possibly the remains of diatoms or flagellates. This mush was only once seen in a herring large enough to have developed a dorsal fin, but unbroken diatom skeletons were occasionally seen in quite large specimens (40 mm.).

Copepods were the main food after the yolk-sac stage, first as nauplii, but very soon as copepodites and the adults of the smaller forms. Up to the end of April 1935 *Pseudocalanus*, *Microcalanus* and *Oithona* were the most important as food. In May *Centropages*, *Temora* and *Acartia* were eaten freely as well.

In the catches from any one station one organism frequently predominated. Thus on May 7 1935 more *Temora* and Cladocera were eaten than any other organism, whereas on May 14 1935 *Centropages* and Cladocera predominated. On May 21 *Centropages* again predominated but *Temora* was nearly as abundant and the numbers of *Pseudocalanus* and *Acartia* had also increased. There was a great change in the following week when the majority of the herring contained little but *Calanus* eggs. The eggs of *Pseudocalanus* and *Calanus* differ but little in size and in the gut of the herring they may be confused with one another or even with other crustacean eggs such as those of Cladocera; they have therefore been lumped together in Table III. At this time, however, the eggs of the second brood of *Calanus* were appearing and there is no doubt that the great majority, averaging 700 in each feeding herring, were those of *Calanus*. The greatest number found in one gut was 1652. In the samples from the following week eggs were much less abundant and nauplii much more so; the single specimen obtained on June 17 contained 33 *Calanus* copepodites.

Cestode larvae and trematodes were frequently found as parasites in the gut. The latter were more common and the incidence appeared to increase as the herring grew, as many as 29–30% being parasitized in the large catches of May 21 and 30. Cestode larvae were less numerous and they too were more frequent in the older herring.

Plankton

On each occasion that herring larvae were caught in any reasonable quantity (except when taken from Keppel Pier) a vertical haul was taken with the $\frac{1}{2}$ m. fine silk standard net and all the zooplankton organisms picked out and counted, usually in the whole sample, for comparison with the analyses made of the gut contents of the herring. At the beginning of 1934 only copepods, copepod nauplii, and cirripede larvae were counted, but later and during 1935 the analysis was extended to include all zooplankton organisms. The results are shown in Table IV.

Since the chief purpose of taking these hauls was for comparison with the food of the young herring it was essential that they should be taken at the same time and place as that in which the young herring were found. This resulted in a considerable loss in uniformity of the hauls, since some were taken close inshore and others in deep water, and in different parts of the area; thus apart from the changes in depth, and therefore length of haul and quantity of water filtered, there would naturally be a change in the type of plankton caught. The hauls are therefore not strictly comparable one with another and are of little value unless taken in conjunction with the analyses of the herring food.

TABLE III. FOOD PER 100 FEEDING HERRING

Date	% feeding	No. feeding examined	Average length in mm.	Plant remains	*Calanus*			*Pseudocalanus*			*Microcalanus*			*Centropages*			*Temora*		
					Nauplii	Copepodites	Adults	Nauplii	Copepodites	Adults	Nauplii	Copepodites	Adults	Nauplii	Copepodites	Adults	Nauplii	Copepodites	Adults
27. iii. 34	5	5	7·6	100†	–	—	—	—	—	—	-	—	—	—	-	—	—	—	—
2. iv. 34	75	24	10·7	67†	4	—	—	75	—	—	—	—	—	—	—	—	—	—	—
9. iv. 34	40	13	12·8	—	—	—	—	15	100	—	—	—	—	—	—	—	—	—	—
*30. iv. 34– 3. v. 34	25	39	21·1	—	—	8	—	26	64	26	—	44	41	—	—	—	—	—	—
30. iv. 34	—	10	18·3	—	—	—	—	—	20	10	-	—	—	—	—	—	—	—	—
10. v. 34	—	1	21·5	—	—	—	—	100	—	—	—	—	—	—	—	—	—	—	—
3. iv. 35	4	1	7·3	—	—	—	—	100	—	—	—	—	—	—	—	—	—	—	—
9. iv. 35	—	8	14·2	25†	13	13	—	—	—	—	—	—	—	25	13	—	—	—	—
16. iv. 35	75	3	16·2	33†	—	—	—	367	—	—	—	—	—	—	—	—	—	—	—
*22. iv. 35 & 24. iv. 35	21	33	20·2	—	21	—	—	142	21	27	—	103	48	3	9	3	—	6	3
23. iv. 35	3	12	21·2	—	—	—	—	8	25	75	—	—	—	—	—	—	—	—	—
29. iv. 35	1	4	25·6	—	100	175	—	—	75	25	—	—	—	—	—	—	—	—	—
¶2. v. 35	15	29	26·2	—	197	—	—	148	14	14	—	255	131	3	3	—	3	7	28
7. v. 35	10	38	26·4	—	—	—	—	3	—	—	—	—	—	3	24	8	3	100	147
14. v. 35	low	73	31·6	—	—	18	—	4	—	5	3	1	—	10	19	190	—	1	4
21. v. 35	—	100	34·0	3	1	44	21	—	10	31	—	32	32	—	73	216	—	38	171
30. v. 35	—	50	36·4	2	2	4	—	—	—	—	—	—	—	4	—	—	—	—	—
5. vi. 35	81	22	37·9	4	17927	41	23	—	9	18	—	4	—	—	—	—	—	4	—
17. vi. 35	—	1	49·0	—	—	3300	—	—	100	800	—	—	—	—	300	800	—	400	100

* Taken off Keppel.
¶ Taken off Wemyss Point.
† These figures indicate the percentage of herring containing green mush.

TABLE III (*continued*)

Date	% feeding	No. feeding examined	Average length in mm.	*Acartia*			*Oithona*			Harpacticoida	Unidentified Copepoda	Cladocera	Cirripede Nauplii	Crustacean eggs	Euphausid larvae	Zoeae	Isopoda	Molluscan larvae
				Nauplii	Copepodites	Adults	Nauplii	Copepodites	Adults									
27. iii. 34	5	5	7·6	—	—	—	—	—	—	—	40	—	—	—	—	—	—	—
2. iv. 34	75	24	10·7	—	—	—	—	—	—	—	38	—			—	—	—	—
9. iv. 34	40	13	12·8	—	—	—	—	—	—	—	31	—	—	—	—	—	—	—
*30. iv. 34– 3. v. 34	25	39	21·1	5	—	10	—	23	5	3	110	3	—	167	—	—	—	3
30. iv. 34	—	10	18·3	—	10	—	—	—	10	10	50	—	—	2680	—	—	—	10
10. v. 34	—	1	21·5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3. iv. 35	4	1	7·3	—	—	—	—	—	—	—	—	—		—	—	—	—	—
9. iv. 35	—	8	14·2	—	—	—	—	—	—	13	38		—	—	—	—	—	—
16. iv. 35	75	3	16·2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
*22. iv. 35 & 24. iv. 35	21	33	20·2	—	—	3	—	67	48	—	42	—	3	24	3	—		—
23. iv. 35	3	12	21·2	—	—	—	—	8	—	—	—	—	—	300	—	—	—	—
29. iv. 35	1	4	25·6	—	—	—	—	—	—	—	50	—	—	—	—	—	—	—
¶2. v. 35	15	29	26·2	—	—	3	—	28	10	—	45	—	10	1107	—	—	—	396
7. v. 35	10	38	26·4	—	8	13	—	—	—	—	5	252	—		—	—	—	3
14. v. 35	low	73	31·6	—	3	34	—	1	—	1	4	200	—	95	—	—	—	27
21. v. 35	—	100	34·0	—	5	71	—	—	—	1	8	27	5	690	—	2	1	36
30. v. 35	—	50	36·4	—	2	8	—	—	—	38	6	78	—	70432	—	—	—	36
5. vi. 35	81	22	37·9	—	18	4		4	—	4	104	59	18	37905	—	—	—	36
17. vi. 35	—	1	49·0	—	100	300	—		—	—	9400		—	100	—	—	—	—

TABLE IV. ZOOPLANKTON IN VERTICAL HAULS WITH $\frac{1}{2}$ M. FINE SILK NET

	1934						1935									
	March			April			April					May				
	13	19	27	2	9	30	3	9	16	23	29	2	7	14	21	30
Calanus copepodites	25	5	7	20	560	21	96	316	444	1744	368	183	339	674	399	478
Pseudocalanus and *Paracalanus*	161	14	176	3150	8170	22	28	285	189	630	57	88	174	205	221	168
Microcalanus	271	37	17	–	750	—	14	—	92	1600	1080	631	385	721	1871	1012
Centropages	8	1	33	70	110	95	10	382	96	52	39	2	21	64	22	48
Temora	13	2	24	70	90	2	9	66	37	28	6	15	374	4	11	4
Acartia	12	4	68	120	80	183	17	132	77	22	117	8	345	476	158	292
Oithona	214	33	39	130	1260	—	130	48	147	206	27	67	26	55	28	16
Harpacticoida	12	4	1	20	40	35	—	5	28	15	53	5	3	7	13	6
Calanus eggs	—	—	—	—	5	1520	25	12	4	20	525	1344	848	592	1424	12340
Calanus nauplii	637	186	1856	9010	9100	303	367	224	540	400	235	964	256	400	392	8570
Other nauplii	32	4	2	–	60	2	350	1440	492	2920	1800	300	536	388	520	1510
Euphausidae				30	120	3	43	35	14	20	7	13	12	1	—	16
Decapoda				—	10	3	1	—	1	—	—	1	1	—	1	1
Appendicularia				110	370	—	54	16	—	4	—	2	—	2	1	7
Polychaete larvae				140	500	—	89	48	56	28	20	5	27	9	19	14
Echinoderm larvae				10	10	—	27	13	6	15	—	5	—	–	8	300
Cladocera				30	100	—	5	54	89	—	79	—	112	22	8	14
Molluscan larvae				—	60	4	23	50	138	1600	450	852	69	1	1	9
Microniscus				—	—	—	—	—	2	3	6	4	4	4	6	3
Fish eggs				20	—	2	10	9	9	12	—	10	3	3	—	12
Chaetognatha				—	—	—	4	7	2	1	—	—	—	—	—	1
Cirripede nauplii	123	84	6	60	—	1	19	79	29	2	1	13	3	3	—	—
Other calanoids	—	18	50	—	20	—	1	2	1	—	2	1	1	2	—	1
Rotifera				780	—	—	—	—	—	—	—	—	–	—	—	—
Medusae				10	10	—	—	12	2	—	–	—	—	—	–	—
Other larvae				100	190	—	—	—	—	—	—	—	–	–	–	—
Cyphonautes				—	—	1	—	2	7	7	3	1	—	—	—	—
Amphipoda				—	—	—	—	—	7	1	—	—	–	—	—	—
Nematoda				—	—	—	—	—	1	—	—	—	—	—	—	—
Total	1508	392	2279	13880	21615	2197	1322	3237	2510	9330	4875	4514	3539	3633	5103	24822

The more important copepods occurred in every haul, with the exception of *Microcalanus* which was absent from three hauls. It may be noted that these hauls were from shallow water fairly close inshore; while not invariably absent from hauls of shallow depth *Microcalanus* always occurred in hauls taken in deeper water.

The total number of organisms was usually less than 5000 but rose on one or two occasions considerably above this figure, the increase being due to the presence of *Calanus* eggs in large quantities during the breeding periods.

Apart from the Copepoda individual species showed occasional sudden increases which lasted for a longer or shorter time. Notable among these outbursts was that of the molluscan larvae which rose from 138 on April 16 1935 to 1600 in the following week, remained fairly high (450, 852) for the two succeeding weeks, falling below 100 a week later. The first two of these hauls were taken in the Kilbrennan Sound, the third and fifth at the Otter Spit; the fourth was taken at Wemyss Point and is therefore possibly not comparable.

Relation between Food and Plankton

The comparison of the plankton analyses with the food taken presents some difficulties. Firstly, since vertical hauls only were taken, they were not representative of the plankton at the particular depth at which the herring were captured. The herring were usually caught fairly near the surface and some copepods, for instance *Microcalanus*, are found mainly in deep water. On the other hand the herring were not necessarily feeding at the depth where they were caught, for the fact that the food was usually in the intestine indicates that digestion had been going on for some time. Secondly, the size of the herring must be taken into consideration, for while they are small they tend to take only the smaller organisms. In Table V therefore, in which the food and the plankton are compared, the food organisms have been arranged in order of their abundance in the herring guts and compared with the common food organisms arranged in order of their abundance in the vertical hauls.

At a length of 10·7 mm. (April 2 1934) the herring were taking only nauplii from a choice of nauplii and *Pseudocalanus*. A week later, at a size of 12·8 mm., *Pseudocalanus* copepodites were included in their diet, and with a further increase of 2 mm. in length (April 9 1935) *Calanus* and *Centropages* were being eaten.

In a few instances (e.g. April 9 1935, May 2 1935) the correlation between gut contents and townettings is very good, and the organisms most frequent in the gut were those most abundant in the vertical haul, but as a rule only a general relationship can be made out.

Although *Calanus* was usually one of the more numerous copepods in the townettings it was not eaten in numbers until the middle of May, when the herring had reached the length of about 30 mm. In 1935 *Oithona* was eaten more often in April and the beginning of May than later, corresponding to its

TABLE V. COMPARISON OF HERRING FOOD AND PLANKTON

Date	No. of herring examined	Average size in mm.	Food organisms arranged in order of abundance: In herring guts	Food organisms arranged in order of abundance: In the plankton
1934 April 2	24	10·7	Nauplii	Nauplii *Pseudocalanus*
,, 9	13	12·8	*Pseudocalanus* Nauplii	Nauplii *Pseudocalanus* *Oithona* *Microcalanus*
,, 30	10	18·3	*Calanus* eggs *Pseudocalanus* *Acartia* *Oithona* Harpacticoida *Calanus* nauplii	*Calanus* eggs Nauplii *Acartia* *Centropages* Harpacticoida *Pseudocalanus* *Calanus*
1935 April 9	8	14·2	Other nauplii *Calanus* *Centropages* *Calanus* nauplii	Other nauplii *Centropages* *Calanus* *Pseudocalanus* *Calanus* nauplii *Acartia*
,, 16	3	16·2	Other nauplii	*Calanus* nauplii Other nauplii *Calanus*
,, 23	12	21·2	*Pseudocalanus* *Oithona* Other nauplii	Other nauplii *Calanus* *Microcalanus* Molluscan larvae *Pseudocalanus* *Oithona*
,, 29	4	25·6	*Calanus* copepodites *Calanus* nauplii *Pseudocalanus*	Nauplii *Microcalanus* *Calanus* eggs *Calanus* *Calanus* nauplii *Pseudocalanus*
May 2	29	26·2	*Calanus* eggs *Microcalanus* Molluscan larvae *Calanus* nauplii Other nauplii *Oithona* *Temora* *Pseudocalanus*	*Calanus* eggs *Calanus* nauplii Molluscan larvae *Microcalanus* Other nauplii *Calanus* *Pseudocalanus* *Oithona* *Temora*
,, 7	38	26·4	Cladocera *Temora* *Centropages* *Acartia* Other nauplii	*Calanus* eggs Other nauplii *Microcalanus* *Temora* *Acartia* *Calanus* *Calanus* nauplii *Pseudocalanus* Cladocera *Centropages*

TABLE V (*continued*)

Date	No. of herring examined	Average size in mm.	Food organisms arranged in order of abundance	
			In herring guts	In the plankton
1935 May 14	73	31·6	*Centropages* Cladocera *Acartia* Molluscan larvae *Calanus* *Temora* *Pseudocalanus* *Oithona*	*Microcalanus* *Calanus* *Calanus* eggs *Acartia* *Calanus* nauplii Other nauplii *Pseudocalanus* *Centropages* *Oithona*
„ 21	100	34·0	Copepod eggs *Centropages* *Temora* *Acartia* *Microcalanus* *Calanus* Cladocera Molluscan larvae	*Microcalanus* *Calanus* eggs Other nauplii *Calanus* *Calanus* nauplii *Pseudocalanus* *Acartia*
„ 30	50	36·4	*Calanus* eggs Cladocera Harpacticoida Molluscan larvae *Acartia* *Calanus*	*Calanus* eggs *Calanus* nauplii Other nauplii *Microcalanus* *Calanus* *Acartia* Echinoderm larvae *Pseudocalanus*

occurrence in the townettings, and *Acartia* was more abundant in both guts and townettings from May 7 onwards. *Centropages* and *Temora* were also eaten more frequently after May 7, but since there was no corresponding increase in their numbers in the townettings this may have been because they were too large to be eaten freely by the younger larvae. The most striking correspondence between gut content and plankton counts is perhaps that already mentioned for May 30 when the second brood of *Calanus* eggs appeared.

The conclusions to be drawn are firstly, that the food taken is dependent on the size of the herring, particularly in the first month; secondly, that having attained the requisite size the larvae may take whatever happens to be present; and thirdly, that although *en masse* they appear to exercise no selection, occasionally one herring may be found with one organism predominant in its gut.

Comparison with Observations elsewhere

The present work on the food of the young herring confirms results already obtained in the North Sea and English Channel. Lebour (1921*b*, 1924, 1933) deals chiefly with the younger stages. She too found that a large proportion of the youngest stages contain no recognizable food, but she also found that larval molluscs, particularly gastropods, were very important for the young herring up to 10 or 12 mm. In the Clyde these did not occur in herring guts at this stage, possibly because they were not numerous in the plankton until the end of April.

The herring examined by Ogilvie (1927) ranged in size from 27·5 to 45·5 mm. and were taken in three hauls, one in April and two in June off the east coast of Scotland. In all three hauls over 90% of the herring were feeding, a percentage very much greater than is usually found in the Clyde. The food consisted almost entirely of copepods, of which *Pseudocalanus elongatus* was most numerous in one catch, *Oithona similis* in the second, and *Eurytemora hirundinoides* in the third. Copepod ova are also mentioned as "fairly abundant" on several occasions. The amount of food per fish is much greater than that in the Clyde fish.

Hardy's (1924) observations cover all stages of the young herring up to and beyond metamorphosis. Although a larger percentage of his herring were feeding (47·8% of the 12·5–42·0 mm. stages) the amount of food taken per fish seems to be much the same as or rather less than that in the Clyde. *Pseudocalanus* was by far the most important copepod. *Temora* and *Microcalanus* occurred in small numbers, but *Calanus*, *Centropages* and *Oithona* were not taken at all at this stage. Hardy suggests that *Calanus* and *Temora*, which were present in the plankton at the time, were not eaten because of their size. In the Clyde, however, an adult *Temora* was eaten by a herring of 22·5 mm. and many by those of 25–30 mm. *Calanus* also was eaten by quite small herring; a Stage I copepodite was found in a herring of 16·5 mm., six Stage I in a herring of 23 mm., Stages IV and V were found in herring of 33 mm., and adults in herring from 35 mm. upwards.

Ogilvie mentions the great increase in the amount of food taken by herring of and over 40 mm. This is confirmed by the examination of the single Clyde herring of 49 mm. which contained 156 copepodites. Apart from this specimen the largest number of copepodites found in any one gut was 69 in a 35 mm. fish (1 *Calanus*, 8 *Pseudocalanus*, 43 *Microcalanus*, 4 *Temora* and 13 *Acartia*), as well as 7 cladocera, 1 lamellibranch larva and 18 copepod eggs.

Weight and Composition

Samples of the herring captured were weighed. Since it proved difficult to keep a sufficient number alive they were usually fixed in neutral formalin immediately after capture and weighed within 1 or at most 2 days. The loss in dry weight due to fixation is small in that time. It is very probable that measurements of the wet weight on fixed material would be unreliable, so dry weight alone was measured. The herring were rinsed with distilled water and dried to constant weight at 105–110° C. During the first few weeks after hatching, the range in size in individual catches was small and a mixed sample was measured and weighed. As the herring became larger, the range in size in individual samples increased; for this reason not only was a mixed sample of the catch taken for weight estimation (Series 1, Figs. 3 and 4) but a series of herring samples of different millimetre size groups was also weighed (Series 2–5, Figs. 3 and 4).

The results of the weighings are shown in Table VI and Fig. 3. As might be expected the curve showing the weight-length relationship is exponential in form. The curve drawn is that for $W = 0{\cdot}0000020L^{4{\cdot}52}$, the theoretical curve derived from the data. Above 40 mm., when the fish are approaching metamorphosis, they are slightly heavier than would be expected. The point at 49 mm. represents one fish which had completely metamorphosed.

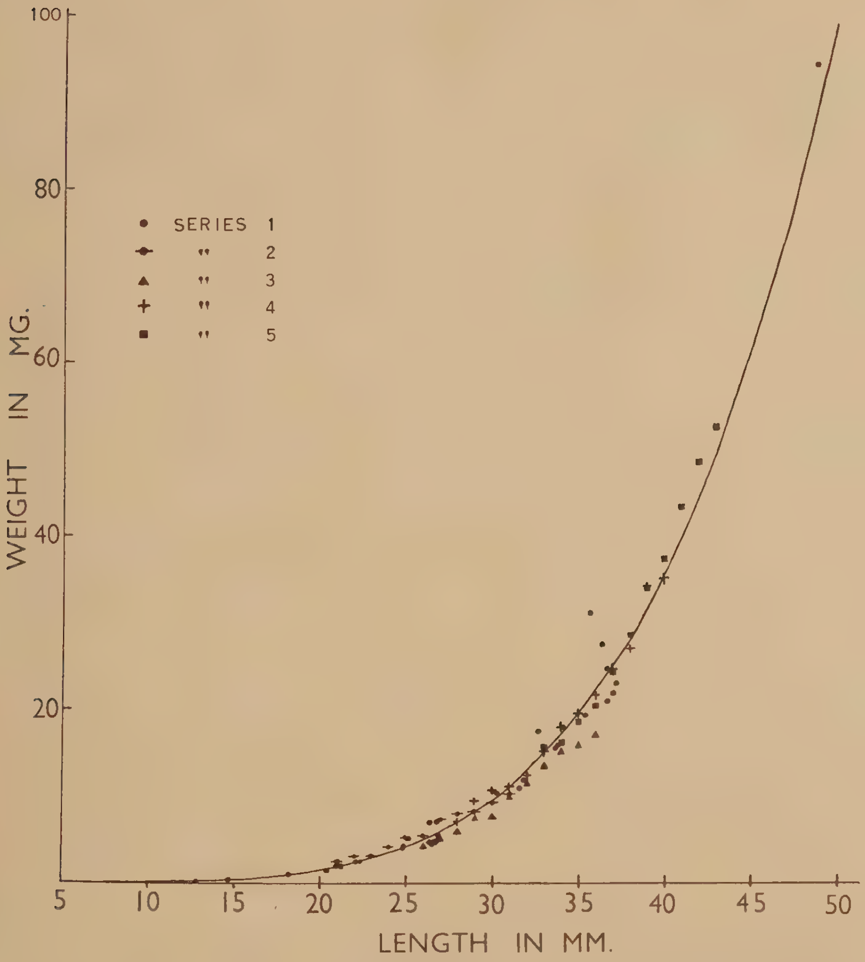


Fig. 3. Relation of weight to length in pre-metamorphosis herring. Series 1, average of a sample of each catch; Series 2, May 7 1935; Series 3, May 14 1935; Series 4, May 21 1935; Series 5, May 30 1935.

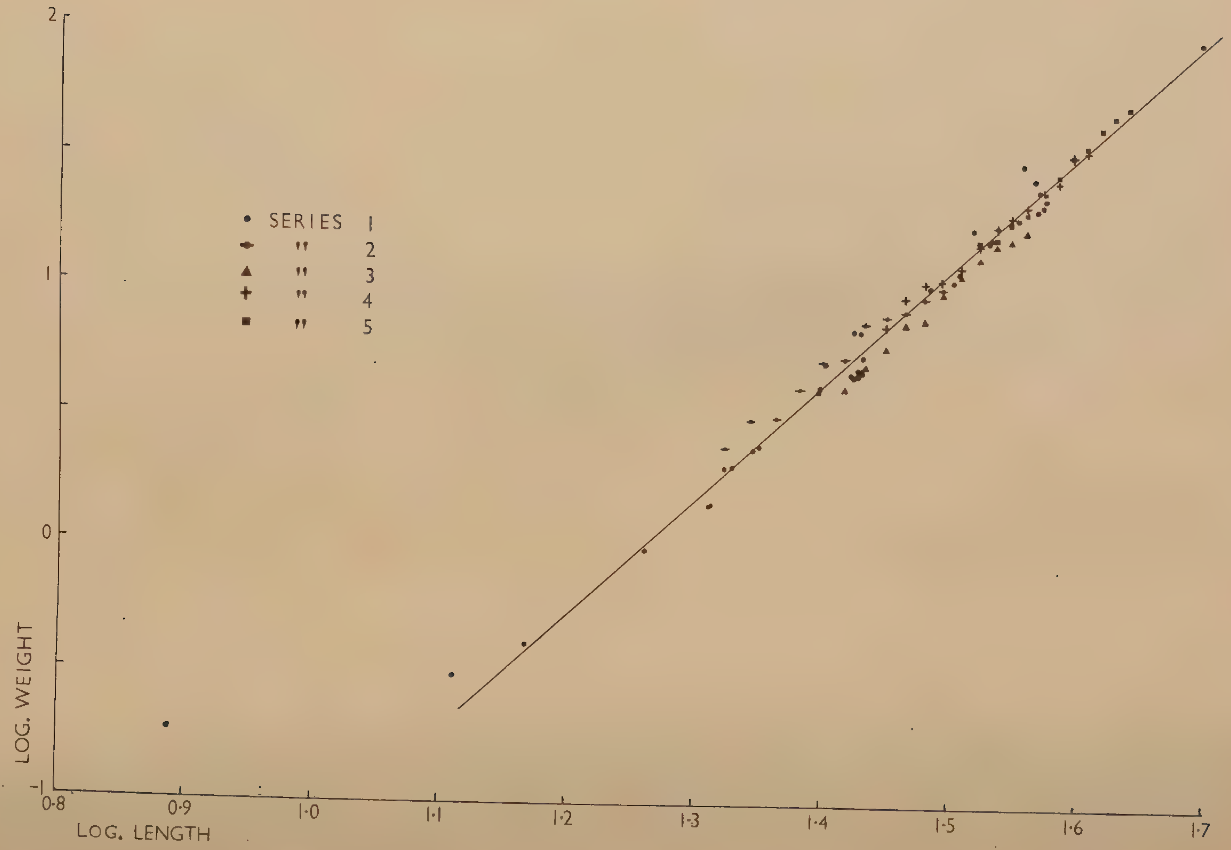


Fig. 4. Relation of logarithm of weight to logarithm of length in pre-metamorphosis herring. Series 1–5 as in Fig. 3.

By plotting the logarithms of the length against the logarithms of the weight it is shown (Fig. 4) that with one exception the points lie on or near a straight line. Excluding this one point the equation of the theoretical straight line was found by the method of least squares to be $Y = 4{\cdot}52X - 5{\cdot}70$, i.e.

$$W = 0{\cdot}0000020L^{4{\cdot}52},$$

where W represents the weight and L the length. The relation between length and weight usually taken for fish is $W = FL^3$, where F is a constant. Since in the present instance the dry weight only was measured, a direct comparison of pre-metamorphosis herring with other fish cannot be made, but by comparing our figures with those given by Fulton (1904) and thus taking the water content as 85 %, we find that the weight is proportional more nearly to the fourth power of the length than to the third.

The first point does not fit the curve (Fig. 4) and has been omitted from the calculations because herring at this size still have a prominent yolk-sac; the weight measurement was thus not truly comparable with those above 10 mm. when the yolk-sac has disappeared.

The fat content of the herring was estimated in samples taken on and after April 23 1935. For this purpose a suitable number of herring was taken while still alive, rinsed in distilled water and transferred to a small quantity of alcohol on board. On returning to the laboratory they were dried and weighed and the fat estimated by Stoddard & Drury's (1929) method.

The results are shown in Table VI and are expressed as percentage of fat in the dried herring. The fat content of pre-metamorphosis fish is much lower than that of adult herring, but there is a rise in fat content as the fish approach metamorphosis. At about 25 mm. the young herring had a fat content of 3·5 %; a sample a week later had 5 % but in the two following weeks it was only 4·3 and 4·7 %. The small sample of May 27 had 5·7 % fat while the large sample of May 30 had 8·5 %. This figure was verified using the Soxhlet ether extraction method. The sample of June 5 which was small in numbers and showed a decrease in size had a lower fat content (4·9 %). It is apparent that while increase in size in pre-metamorphosis herring is accompanied in general by an increase in fat content, the rate of increase is not regular. This may be due to inaccurate sampling of the catch or to variations in the condition of the herring themselves.

EXPERIMENTAL WORK

An attempt was made to rear larval herring in the aquarium, from spawn obtained either naturally or artificially, with the object of making experiments on their metabolism. As other observers have found, it is almost impossible to keep the larvae alive after they have lost the yolk-sac. After this stage there is no increase in length and an actual loss in weight. Experiments with newly hatched larvae, however, are probably reliable.

TABLE VI. WEIGHT AND FAT CONTENT OF HERRING

Date	Place	Size mm.	Dry weight mg.	Fat % dry weight
1934				
March 19	Iron Rock Ledges	7·6*	0·186	—
April 9	Machrie Bay	12·9	0·310	—
,, 30	Keppel	20·5	1·47	—
,, 30	Machrie Bay	18·2	0·97	—
May 2	Keppel	20·4	1·45	—
1935				
April 9	Machrie Bay	14·7	0·41	—
,, 22	Keppel	21·3	2·06	—
		21·0	2·03	
,, 23	Skipness	22·1	2·40	—
		22·3	2·47	
,, 29	Barmore	24·8	4·08	
		24·9	4·24	
		25·1	5·23	3·5
		26·9	5·55	
,, 29	Otter Spit	26·6	4·74	—
		26·9	4·98	
May 2	Wemyss Point	26·6	4·93	—
		26·3	4·75	
		26·5	4·68	
		26·8	4·83	
,, 7	Otter Spit	26·8	6·95	
		26·3	7·01	5·0
		30·3	10·41	
Series 2		21	2·45	
		22	3·13	
		23	3·19	
		24	4·17	
		25	5·31	
		26	5·50	
		27	7·50	
		28	7·96	
		29	8·40	
		30	9·42	
		31	10·27	
May 14	Otter Spit	31·6	10·98	
		31·8	11·84	
		34·1	17·97	4·3
		32·7	17·49	
Series 3		26	4·17	
		27	5·10	
		28	6·02	
		29	7·52	
		30	7·69	
		31	9·88	
		32	11·55	
		33	13·51	
		34	15·19	
		35	15·91	
		36	17·18	
May 21	Otter Spit	33·7	15·66	
		33·8	16·01	
		36·4	27·52	4·7
		36·7	24·78	

* In the first sample the tail fin was not included in the measurement.

Table VI (*continued*)

Date	Place	Size mm.	Dry weight mg.	Fat % dry weight
1935				
Series 4		28	7·28	
		29	9·52	
		30	10·76	
		31	11·16	
		32	12·45	
		33	15·20	
		34	18·12	
		35	19·61	
		36	21·74	
		37	24·83	
		38	27·06	
		39	34·27	
		40	35·37	
May 27	Otter Spit	35·4	19·36	5·7
„ 30	Otter Spit	36·7	21·03	8·5
		37·0	21·88	8·5*
		37·2	23·15	
Series 5		33	15·80	
		34	16·23	
		35	18·65	
		36	20·46	
		37	24·36	
		38	28·73	
		39	34·21	
		40	37·41	
		41	43·66	
		42	48·67	
		43	52·87	
June 5	Otter Spit	35·7	31·15	4·9
„ 17	Barmore	49	94·6	—

* Soxhlet extraction.

For an experiment on oxygen consumption, larvae were obtained from spawn which was dredged on the Iron Rock Ledges and hatched in the laboratory. Hatching had taken place over the previous five days and the length of the fifty larvae used varied from 5·5 to 10 mm. (average size 8·3 mm.). A few had lost the yolk-sac and its size varied considerably in the others. Larval herring taken on the Iron Rock Ledges on the previous day whose average size was 7·8 mm. weighed on an average 0·20 mg.

Thirty herring were put in each of four bottles of filtered sea water of which two were kept in the dark (at 10° C.) and two in sunlight (at 8–12° C.) for 6 hr. The initial oxygen content of the bottles was 6·6 ml. per litre. Those in the dark used 0·46 and 0·44 ml. per 1000 per hr. and those in the light 0·40 and 0·33 ml. per 1000 per hr. A control experiment showed that there was not enough phytoplankton in the filtered sea water to affect the results either in the dark or in the light.

Larvae from the same source were used for another respiration experiment 19 days later, but used only 0·25 and 0·21 ml. per 1000 per hr. The yolk-sac had completely disappeared, the size ranged from 9·5–11 mm., and the weight was only 0·12 mg. per herring as compared with 0·31 mg. for herring in the sea about the same time. As is shown in Table VI herring even in the yolk-sac stage in the sea weigh more than this (0·186 mg.). This experiment showed that the artificially reared herring were not now growing normally.

The larvae used in the first respiration experiment were afterwards used to determine the lethal temperature. Five herring were put in each of ten small bottles and these were kept in a tank whose temperature was controlled by a thermostat. The temperature at the beginning of the experiment was 11° C. At the end of each hour the condition of the herring was noted and the temperature then raised by 1° C.

With the increase of temperature, activity increased up to 23° C. after which they became sluggish or moribund. At 26° C. five bottles were taken out of the tank and allowed to cool. The remaining five bottles were raised to 27° C. After an hour at this temperature all the herring with one exception were moribund. They were then allowed to cool. By next morning, of those removed at 26° C. practically all had recovered and of those removed at 27° C. about half had recovered. The results indicate that larval herring are affected by a temperature above 24° C. but could survive, for at least a short time, a temperature of 26° C. Gross (1937) has suggested that larval herring are very susceptible to sudden change of temperature, but the above results do not seem to confirm this.

The oxygen content of one of the bottles at 27° C. was 5·13 ml. per litre showing that lack of oxygen can not have affected the results.

We are indebted to the Fishery Board for Scotland who arranged the forwarding of weekly reports on the Clyde herring fishery, and to Mr H. J. Buchanan-Wollaston who helped us with the statistical work. We also wish to thank the crew of the *Nautilus* for their constant help in the collection of the material.

SUMMARY

1. Samples of herring from the Clyde sea-area were obtained weekly from the time of hatching in March until metamorphosis in June.

2. The rate of growth was regular, about 3 mm. in length per week; the development was similar to that described from elsewhere.

3. The herring which hatched off the south-west of Arran gradually moved northwards into the mouth of Loch Fyne and remained there until metamorphosis.

4. The proportion feeding was usually small. The food consisted mainly of copepods, both young stages and adults. The size of the food organisms eaten depended roughly on the size of the herring.

5. Plankton hauls taken at the same time as herring were captured showed that there was a general relationship between plankton and gut contents.

6. The relationship of the dry weight (W) of the herring to the length (L) is given by the equation $W = 0{\cdot}0000020L^{4{\cdot}52}$. The fat content was low but increased as the fish approached metamorphosis.

7. The oxygen consumption of herring larvae reared in the laboratory was measured. These larvae did not tolerate a temperature above about 26° C.

REFERENCES

CLARK, R. S., 1933. Herring larvae. The mixing of the broods in Scottish waters. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. LXXXV, Part 3, pp. 11–18.

FULTON, T. W., 1904. The rate of growth of fishes. *22nd Ann. Rep. Fish. Bd. Scotland, Sci. Invest.*, pp. 141–241.

—— 1906. On the growth and age of the herring (*Clupea harengus*). *24th Ann. Rep. Fish. Bd. Scotland, Sci. Invest.*, pp. 293–342.

GROSS, F., 1937. Notes on the culture of some marine plankton organisms. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 753–68.

HARDY, A. C., 1924. The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. VII, No. 3, pp. 1–53.

LEBOUR, M. V., 1921*a*. The larval and post-larval stages of the pilchard, sprat and herring from the Plymouth district. *Journ. Mar. Biol. Assoc.*, Vol. XII, pp. 427–57.

—— 1921*b*. The food of young clupeoids. *Journ. Mar. Biol. Assoc.*, Vol. XII, pp. 458–67.

—— 1924. The food of young herring. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 325–30.

—— 1933. The importance of larval mollusca in the plankton. *Journ. Cons. Int. Explor. Mer*, Vol. VIII, pp. 335–43.

MASTERMAN, A. T., 1896. Note on the rate of growth, larval and post-larval forms of the herring. *14th Ann. Rep. Fish. Bd. Scotland, Sci. Invest.*, pp. 294–302.

MEYER, H. A., 1878. Beobachtungen über das Wachsthum des Herings im westlichen Theile der Ostsee. *Jahresbericht der Komm. z. wiss. Untersuch. der deutschen Meere in Kiel*, 4–6. Jahrg., pp. 227–252.

OGILVIE, H. S., 1927. Observations on the food of the post-larval herring from the Scottish coast. *Fisheries, Scotland, Sci. Invest.*, No. I, pp. 1–10.

RUNNSTRØM, S., 1934. The pelagic distribution of the herring larvae in the Norwegian waters. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. LXXXVIII, No. V, pp. 1–6.

RUSSELL, F. S., 1930. The vertical distribution of marine macro-plankton. IX. The distribution of the pelagic young of teleostean fishes in the daytime in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 639–76.

STODDARD, J. L. & DRURY, P. E., 1929. A titration method for blood fat. *Journ. Biol. Chem.*, Vol. 84, pp. 741–48.

WILLIAMSON, H. C., 1910. Experiments to show the influence of cold in retarding the development of the eggs of the herring (*Clupea harengus*, L.), plaice (*Pleuronectes platessa*, L.) and haddock (*Gadus aeglefinus*, L.). *27th Ann. Rep. Fish. Bd. Scotland*, Part III, *Sci. Invest.*, pp. 100–28.

—— 1911. Report on the retardation of the development of the ova of the herring. *Fisheries, Scotland, Sci. Invest.*, 1910, No. II, pp. 1–12.

THE METALLIC CONSTITUENTS OF MARINE GASTROPODS

By R. A. McCance, M.D., Ph.D. and L. R. B. Shackleton, Ph.D.

Biochemical Laboratory, King's College Hospital, London

In 1933 McCance & Shipp (*a*) pointed out that one of the common marine molluscs, *Littorina littorea*, contained between 346 and 507 mg. of magnesium per 100 g. of live weight. While these enormous concentrations of magnesium were not confined to any one organ, the gonads and liver appeared to contain rather more than the foot and mantle. The object of the present paper is to report upon the mineral composition of some of the species allied to *L. littorea* and also of some of the other gastropods. The chemical methods used have been described in previous publications (McCance & Shipp 1933 *b*; McCance, Widdowson & Shackleton, 1936). The animals were all obtained from the Marine Biological Association at Plymouth, and the analytical results are set out in Table I, the approximate composition of sea water of 33 °/₀₀ salinity being added for comparison (Harvey, 1928). When it was necessary to do so, the shells were broken to extract the animals, and in some instances fragments of shell were included in the material taken for analysis. The figures given for calcium, therefore, are in some instances too high, and in one or two cases the amount of calcium carbonate in the material taken has led to appreciable errors in the true water content, e.g. in *L. neritoides*.

The results which call for comment seem to be:

(1) The animals always contain less sodium than the surrounding water, but the amount of sodium per 100 g. of body water varies on both sides of, and is often not far from the amount of sodium per 100 g. of sea water.

(2) Judged by vertebrate standards, many of the animals contain surprisingly large amounts of potassium. Some of them, notably *L. rudis* and *Lacuna vincta*, contain more than 1000 mg./100 g., and it would be of considerable interest to know how this potassium was combined.

(3) The calcium in some of these animals may be quite small in amount but is always greater than that in the surrounding sea water, and may be extremely high even in animals in which shell contamination can be absolutely excluded. The most striking instances of this are the two Nudibranchia, *Jorunna* and *Archidoris*, the latter of which contains almost 2·5 % of calcium.

(4) The large amount of magnesium in the winkle (*Littorina littorea*) is confirmed. In *L. neritoides* and *L. rudis* the magnesium is also very high, but these magnesium contents are not peculiar to the Littorinas, for both *Nucella lapillus* and *Scaphander* contain similar amounts of magnesium, and in *Jorunna*, and particularly *Archidoris*, the magnesium concentrations are enormous

(McCance & Masters, 1937). It would seem that these marine molluscs may be divided into three groups according to their magnesium contents. The first, as illustrated by *Aeolidia*, *Mytilus edulis* and *Ostrea edulis* (see McCance & Shipp, 1933 *a*) contain much less magnesium than the surrounding water, and it is clear that in this respect their body water must differ radically in composition from the sea. In the second group, of which *Pecten maximus*, *Cardium edule* (McCance & Shipp, 1933 *a*), *Buccinum undatum*, *Aplysia* and *Sphaerostoma* are examples, the concentration of magnesium in the animals is less than that in the surrounding water, but the concentration of magnesium in their body water appears to be close to that in sea water. The third group (*Archidoris*, *Jorunna*, *Littorina littorea*, etc.) contains huge concentrations of magnesium. Nothing is known of the state of combination of the metal except in the case of *Archidoris* (McCance & Masters, 1937), and even in this instance the function of the metal remains a matter of conjecture.

TABLE I

			Composition per 100 g. of live weight (mg.)					
Order and name	Organ	Water g.	Na	K	Ca	Mg	Fe	Cu
MESOGASTROPODA								
Littorina littorea	Foot and gut	69·5	688	425	821	456	25·8	1·77
	Gonad and liver	64·0	702	425	913	519	25·6	2·52
L. littoralis	Foot and gut	70·0	420	654	1480	150	9·4	4·73
	Gonad and liver	60·3	471	778	4350	256	15·2	9·13
L. neritoides	Whole animal	61·0	429	737	4500	332	26·5	10·2
L. rudis	Foot and gut	67·8	536	1000	1285	256	15·6	3·1
	Gonad and liver	62·7	695	728	3700	342	37·5	8·1
Lacuna vincta	Whole animal	69·5	724	1110	472	127	14·1	8·1
ARCHAEOGASTROPODA								
Patella vulgata	Whole animal	74·7	466	445	334	66·8	34·0	0·97
P. athletica	Whole animal (except radula)	79·2	432	213	348	84·1	15·3	0·67
Calliostoma zizyphinum	Foot and gut	74·2	678	383	278	90	19·8	5·4
	Gonad and liver	73·4	755	343	362	130	111·0	11·0
STENOGLOSSA								
Buccinum undatum	Foot and gut	73·2	431	413	75	114	2·5	0·55
	Gonad and liver	73·8	774	810	201	100	12·0	54·8
Nucella lapillus	Foot and gut	69·5	418	288	483	230	7·5	1·5
	Gonad and liver	64·1	548	217	378	208	12·0	5·3
TECTIBRANCHIA								
Scaphander lignarius	Whole animal	78·0	565	450	316	282	6·60	0·50
Aplysia punctata	Whole animal (excluding gastric plates)	86·0	635	240	115	114	10·4	0·70
NUDIBRANCHIA								
Aeolidia papillosa	Whole animal	79·0	—	—	62	60	12·5	—
Sphaerostoma hombergi	Whole animal	89·0	—	—	81	127	2·8	—
Jorunna tormentosa	Whole animal	85·0	450	240	580	620	15·7	2·16
Archidoris britannica	Whole animal	78·0	778	368	2460	1580	8·57	1·56
Sea water (from Harvey, 1928)		96·7	1033	37·9	41·3	128	—	—

(5) The concentrations of iron vary from 2·5 to 111 mg./100 g. according

to the species and organ. The radulae of the Patellidae have formed the basis of a special study (Jones, McCance & Shackleton, 1935).

(6) Judged by mammalian standards, some of the copper concentrations are very high. The gonad and liver of *Buccinum* may be cited in illustration. At present one can only record the facts without reference to function.

The authors are indebted to Dr E. I. Jones for his collaboration and assistance, particularly in the dissection of the specimens. The work could not have been carried out without the co-operation of the staff of the Marine Biological Association at Plymouth. Certain of the costs were defrayed by the Medical Research Council.

SUMMARY

The sodium, potassium, calcium, iron and copper have been determined in sixteen marine gastropods, and the results are briefly discussed. A noteworthy finding is the large amount of potassium, calcium and (or) magnesium which may be present in these animals. *Lacuna vincta* for example may contain over 1·1 % of potassium, *Archidoris britannica* 1·58 % of magnesium per 100 g. of live weight.

REFERENCES

HARVEY, H. W., 1928. *Biological Chemistry and Physics of Sea Water*, p. 36. Camb. Univ. Press.

JONES, E. I., MCCANCE, R. A. & SHACKLETON, L. R. B., 1935. The role of iron and silica in the structure of the radular teeth of certain marine molluscs. *Journ. Exper. Biol.*, Vol. 12, p. 59.

MCCANCE, R. A. & MASTERS, M. E. M., 1937. The chemical composition and the acid base balance of *Archidoris britannica*. *Journ. Mar. Biol. Assoc.*, Vol. XXII, p. 273.

MCCANCE, R. A. & SHIPP, H. L., 1933 *a*. The magnesium and other inorganic constituents of some marine invertebrates. *Journ. Mar. Biol. Assoc.*, Vol. XIX, p. 293.

—— —— 1933 *b*. The chemistry of flesh foods and their losses on cooking. *Spec. Rep. Ser. Med. Res. Counc.*, London, No. 187.

MCCANCE, R. A., WIDDOWSON, E. M. & SHACKLETON, L. R. B., 1936. The nutritive value of fruits, vegetables and nuts. *Spec. Rep. Ser. Med. Counc.*, London, No. 213.

THE CHEMICAL COMPOSITION AND THE ACID BASE BALANCE OF *ARCHIDORIS BRITANNICA*

By R. A. McCance, M.D., Ph.D. and M. Masters, B.Sc.

Biochemical Department, King's College Hospital, London

(Plate XVII)

The unusual amounts of calcium and magnesium discovered by McCance & Shackleton (1937) in the nudibranch, *Archidoris britannica*, raises a number of interesting questions: Why are the metals there in such quantities? What, if any, is their function? With what are they combined? It was accordingly decided to make a more detailed study of this gastropod and to supply an answer at any rate to the last question.

The animals were obtained alive from the Marine Biological Association at Plymouth. About forty animals have been used for this work, and the practice has been to get about eight sent at one time and to pool them for analysis. The batches have differed little in composition or behaviour. The animals were prepared for investigation as follows: Each was separately removed from sea water, rinsed in distilled water and dried quickly on a cloth. A circular opening was then made in the back and the whole of the visceral mass removed and placed in a separate dish. The visceral cavity was then rinsed out with distilled water and dried. A characteristic feature of the animals is the enormous quantity of mucus secreted after this treatment. On one occasion, for instance, 80 g. of body tissue secreted 24·1 g. of mucus in about 1½ hr. As first secreted the mucus is very viscous but after 2 hr. or so becomes much more fluid and can be withdrawn from the dish by a pipette. The viscera secrete little or no mucus.

METHODS

Water was determined by drying to constant weight at 100° C.; fat by weighing the ether-soluble material removed by 12–24 hr. soxhlet extraction. Glycogen was determined by a micro-Pfluger method (Lawrence & McCance, 1931). The methods used for total nitrogen, phosphorus, chlorine, sodium, potassium, calcium, magnesium, iron and copper have been described by McCance & Shipp (1933) or McCance, Widdowson & Shackleton (1936). Inorganic sulphate was determined as $BaSO_4$. Carbonates and bicarbonates in the solid tissue were decomposed with acid at 37° C., and the CO_2 evolved was carried over by a stream of air into potash bulbs and determined gravimetrically. The conventional precautions were taken and the method gave satisfactory results on pure chemicals. CO_2 in the mucus was determined by

Van Slyke's technique (Harrison, 1937). Strontium was estimated by precipitation of the oxalate and titration of the latter with permanganate. The calcium was previously removed by treating the mixed nitrates with alcohol (Treadwell & Hall, 1935). Fluorine was determined by Willard & Winter's (1933) method. *p*H values were determined colorimetrically in capillary tubes by a slight modification of the B.D.H. Capillator method. Glycogen was determined on fresh material, sampled immediately after removal of the viscera. All analyses of mucus were made on the liquid material; other analyses, except where expressly stated, were carried out on dried material. All analytical procedures, including the initial sampling, were carried out in duplicate.

RESULTS

Before entering into any presentation or discussion of results it is advisable to state that the *p*H of these animals, of the mucus they secrete and of their vascular fluids appears to be the same as that of sea water.

TABLE I. COMPOSITION OF THE BODY TISSUE OF *ARCHIDORIS BRITANNICA*

Protein (N × 6·25)	29·0 %
Fat	1·8 %
Glycogen	1·3 %
Mineral matter (as set out below)	59·7 %

	g.	m.eq.		g.	m.eq.
Na	4·35	190	Cl	7·85	222
K	0·86	22	F	3·00	159
Ca	11·38	569	P (as PO_4)	0·8	13
Sr	0·48	11	Inorg. S (as SO_4)	0·93	19
Mg	6·8	570	CO_3	23·2	775
Totals	23·87			35·78	

Total dry matter accounted for = 91·8
Total base found = 1362 m.eq./100 g. dry matter
Total acid found = 1188 „
Difference 164 „

N.B. Silicon has been looked for and found to be present only in traces.

In preliminary experiments animals were prepared as already described. Shavings of skin and superficial tissue from the back and sides, the remainder of the body tissue with its secreted mucus, and the visceral mass were analysed separately for metallic radicles. This made it clear that the body and the skin, but not the visceral mass, contained the large concentrations of calcium and magnesium. It is unnecessary to give these figures in detail, for similar figures for the guts and body were obtained on other batches of animals, and are given later (Tables I & II). The skin shavings differed inappreciably from the body tissue except that they contained more sodium, possibly due to incomplete removal of sea water, and rather more iron and copper. Table I gives the composition of mixed skin and body tissue as determined by analysis. The material was weighed out before the secretion of mucus had really begun. All constituents, however determined, are calculated as a percentage of the dry matter which itself formed 17·6 % of the total fresh weight.

The composition of this tissue is very unusual; regarded from mammalian standpoints it is fantastic. The most striking features are perhaps: (1) The total amount of mineral matter in a tissue possessing no obviously calcified structure such as a shell or gastric plates. The amount of calcium and magnesium is particularly striking, and it is to these elements that the great excess of mineral matter is due. (2) The presence of 3 % of fluorine. This element was recognized chemically and determined quantitatively before Fox & Ramage's (1931) report of its presence by qualitative spectrographic analysis was discovered. (3) The presence of strontium. This element might have been extraordinarily difficult to detect had it not been for the work of Fox & Ramage.

TABLE II. COMPOSITION OF THE BODY TISSUE AFTER REMOVAL OF THE SECRETED MUCUS, OF THE MUCUS ITSELF AND OF THE VISCERAL MASS

All data refer to fresh weight.

	Body	Mucus	Visceral mass
Water	83·1 g./100 g.	96·0 g./100 c.c.	72·0 g./100 g.
Nitrogen	1·0 „	0·048 „	1·66 „
Fat	1·8 „	—	5·86 „
Ash (residue after combustion)	—	3200 mg./100 c.c.	3300 mg./100 g.
Na	560 mg./100 g.	975 „	348 „
K	136 „	51 „	505 „
Ca	2000 „	53 „	190 „
Sr	85 „	—	—
Mg	930 „	136 „	115 „
Fe	1·3 „	—	42 „
Cu	2·4 „	—	15 „
Cl	953 „	1740 „	1000 „
F	410 „	Tr. or 0	Tr. or 0
P (as PO_4)	126 „	Tr.	877 „
Inorg. S (as SO_4)	42·2 „	—	185 „
HCO_3 (as CO_3)	4500 „	32·7 „	Tr. or 0

Only some 92 % of the dry matter has been accounted for, which may very well be due to the factor 6·25 not being correct for the proteins in *Archidoris*. The amount of nitrogen in mucin (submaxillary) is stated to be only 11·2 % and of mucins generally 11–13 % (Oldfeldt, 1936). The body of *Archidoris* certainly contained large amounts of mucus so that the factor 6·25 is probably too low for this tissue. Hence the amount of protein (29 %) given in Table I may be less than the actual amount present. On the other hand, there is a difference of 164 m.eq. between the total inorganic acid and base which have been accounted for (Table I) so that some of the missing solids may be organic acids. If so their average combining weight must be quite low, i.e. of the order of 53.

An important biological consideration is the state of combination of the CO_2 in the living tissue, i.e. is it present as carbonate or bicarbonate?

To settle this, CO_2 was determined in one batch of animals (*a*) in the fresh state, (*b*) after drying to constant weight at 100° C. The results, calculated to a fresh-weight basis, were as follows: CO_2 in the living state, 4·14 g./100 g., and after drying at 100° C., 4·11 g./100 g. There was therefore very little loss of CO_2 on drying and it is concluded therefrom that the initial form of combination was the carbonate. This is supported by the histological examinations.

Work has also been carried out on the composition of the mucus and of the visceral mass. It is recognized that the analysis of the last is not of the same value as an analysis of the individual organs would have been, but its composition makes an interesting comparison with that of the body tissue and the mucus. The results calculated in each case on the basis of fresh weight are given in Table II. It might have been better to calculate some of the inorganic constituents to a dry-weight basis and others as a percentage of the body water, but this can be done by those interested from the figures given. The animals used for the compilation of Table II were not the same as those used for Table I. The data in Table II are in most instances the mean results obtained from two different batches of animals. It will be observed that the mucus and the visceral mass differ radically in composition from the body tissue. The differences in water, nitrogen and fat are in the direction, and of the order to be expected. The differences in the mineral constituents require more comment. The general inorganic make up of the mucus resembles sea water, and it is evidently composed essentially of the mixed chlorides of sodium, potassium, calcium and magnesium. Some sulphates were no doubt present, but were not determined owing to lack of material. It is a true extracellular fluid in containing sodium rather than potassium salts, the potassium in the animal evidently being associated, as one would expect, with the cellular tissue of the body and the visceral mass. The inorganic constituents of the body have already been described. The mineral matter of the visceral mass, which is probably mainly glandular tissue, makes a strong contrast. The calcium is relatively trifling in amount, potassium occupies a much more prominent role, and chlorides and phosphates make up the acid radicles. Carbonates are conspicuous by their absence. The acid base balance of the visceral mass is given in Table III for comparison with Table I.

TABLE III. ACID BASE BALANCE OF THE VISCERAL MASS CALCULATED TO A DRY-WEIGHT BASIS

	m.eq./100 g.		m.eq./100 g.
Na	54	Cl	101
K	46	P	51
Ca	34	HCO_3	—
Mg	34	SO_4	14
	168		166

Discussion

There is no doubt that the striking feature of this animal is the enormous concentrations of calcium and magnesium to be found in the body tissues and the acid radicles with which they are combined. Histological preparations of the animal, fixed in absolute alcohol, show that the subcutaneous tissue is very loose, and in sections which have been treated with acid there are a large number of tubular spaces (Pl. XVII, fig. 1). These spaces, which vary considerably in size and number, may be collected together in groups of sixteen or more, or scattered diffusely through the tissue. They are not lined by a continuous layer of cells, and the walls are often very thin and appear quite acellular. Occasionally the spaces are filled with what appears to be a radially arranged framework (Pl. XVII, fig. 4). Sections prepared without any contact with acid show the spaces filled with heavily mineralized material somewhat resembling casts of the renal tubules, which in cross-section are marked by concentric lines, and occasionally by radial fracture (Pl. XVII, fig. 3). Where the spaces have been cut longitudinally the mineral masses appear columnar with longitudinal striations. Sometimes the longitudinal columns show transverse fractures. These appearances suggest that the mineral material has been laid down by continuous deposition. Examined superficially the mineral deposits may resemble large crystals. The significance of these mineral agglomerations must remain for the present one of the many unsolved problems of mineral metabolism, but there are one or two points worthy of consideration. In the first place it is difficult to believe that to carry about so much mineral matter and to derive no protection therefrom can possibly have much survival value. *Archidoris britannica* is considered to have lost its shell somewhere in the course of its evolution. Possibly it never thereafter acquired the necessary excretory mechanism for dealing with its ingested calcium. The loss of the property to form a shell must after all have a profound influence upon an animal's mineral metabolism, and in this connexion it is worth noting the gastric plates of certain other gastropods with very reduced shell coverings. On the other hand, calcified spicules are found in animals which never possessed a shell (e.g. didemnid tunicates and even *Alcyonium*), so that there may be no real connexion between the two. It is possible that the retention of magnesium is in some way associated with that of calcium. It is suggestive that the two metals should be present in both the solid tissues in equimolecular amounts (Tables I and III). This, however, may be merely a species peculiarity, for it is not the case in *Jorunna tormentosa* (Cuvier) (McCance & Shackleton, 1937) where the magnesium exceeds the calcium, or in *Littorina littorea* (an animal with a thick shell) where certain of the body tissues may contain much higher concentrations of magnesium than of calcium (McCance & Shipp, 1933). It is perhaps worth noting that the land snail has been found to contain more magnesium than other land animals, and much more magnesium than calcium (Takamatsu, 1936). It seems just conceivable that these large quantities of carbonates are accumulated for their buffering action.

The authors are indebted to L. R. B. Shackleton and A. W. Haynes for assistance at various stages of the investigation, and also to Dr Robison, Miss Murray, Mr D. A. Webb and others for suggestions made at various times. Certain of the costs were defrayed by the Medical Research Council.

Summary

The body of *Archidoris britannica* contains *very* high concentrations of calcium and magnesium which appear to be combined mostly with CO_3 and fluoride. The bulk of these materials are in solid deposits throughout the submucous tissue. Sodium chloride and potassium phosphate account for most of the residual mineral matter.

The mucus secreted by the body has an inorganic composition resembling sea water.

The visceral mass contains only one-tenth as much calcium and magnesium as the body. The predominating bases are potassium and sodium and the acid radicles are essentially chlorides and phosphates.

REFERENCES

Fox, H. M. & Ramage, H., 1931. A spectrographic analysis of animal tissues. *Proc. Roy. Soc.* B, Vol. 108, p. 157.

Harrison, G. A., 1937. *Chemical Methods in Clinical Medicine*, p. 197. Churchill, London.

Lawrence, R. D. & McCance, R. A., 1931. The effect of starvation, phloridzin, etc., on the distribution of glycogen in the rat. *Biochem. Journ.*, Vol. 25, p. 570.

McCance, R. A. & Shackleton, L. R. B., 1937. Metallic constituents of marine gastropods. *Journ. Mar. Biol. Assoc.*, Vol. xxii, p. 269.

McCance, R. A. & Shipp, H. L., 1933. Chemistry of flesh foods and their losses on cooking. *Spec. Rep. Ser. Med. Res. Counc.*, No. 187.

—— —— 1933. Magnesium and other inorganic constituents of some marine invertebrates. *Journ. Mar. Biol. Assoc.*, Vol. xix, p. 293.

McCance, R. A., Widdowson, E. M. & Shackleton, L. R. B., 1936. The nutritive value of fruits, vegetables, and nuts. *Spec. Rep. Ser. Med. Res. Counc.*, No. 213.

Oldfeldt, C. O., 1936. Physikalisch-chemische Untersuchungen an einigen Mucinen und Mucoiden. *Hoppe-Seyl. Z. f. Physiol. Chem.*, Vol. 240, p. 249.

Takamatsu, M., 1936. Kalk und Magnesiumgehalt im Fleisch der verschiedenen Tiere. *Hoppe-Seyl. Z. f. Physiol. Chem.*, Vol. 238, p. 99.

Treadwell, F. P. & Hall, W. T., 1935. *Analytical Chemistry*, Vol. 2, p. 93. John Wiley, New York.

Willard, H. H. & Winter, O. B., 1933. Volumetric method for the determination of fluorine. *Indust. Eng. Chem. Anal. Ed.* Vol. 5, pp. 7–10.

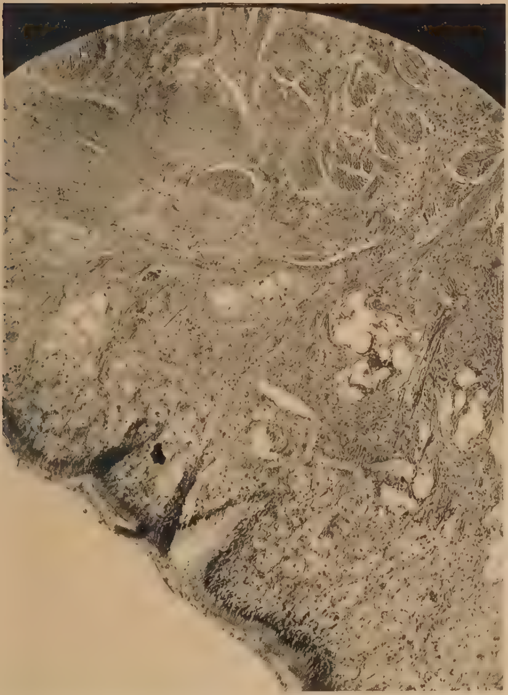
EXPLANATION OF PLATE XVII

Fig. 1. Section of *Archidoris britannica* which has been treated with acid, showing the large number of tubular spaces. Stained with haematoxylin and eosin. × 125.

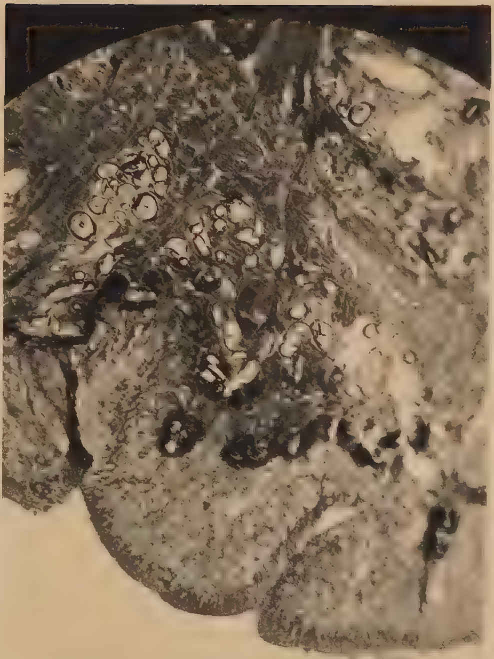
Fig. 2. Section of *Archidoris britannica* prepared without any contact with acid and showing the mineral deposits. Stained with haematoxylin and eosin. × 125.

Fig. 3. Section of *Archidoris britannica* prepared without any contact with acid, showing the mineral deposits and the concentric markings on those deposits which have been cut transversely. Stained with Van Giesen. × 300.

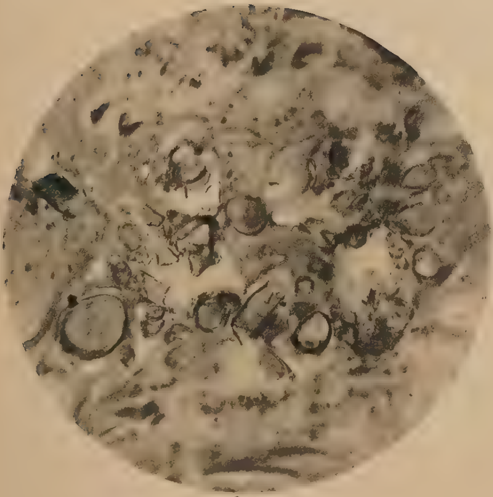
Fig. 4. Section of *Archidoris britannica* which has been treated with acid, showing the spaces filled with what appears to be a radially arranged framework. Stained with methylene blue. × 300.



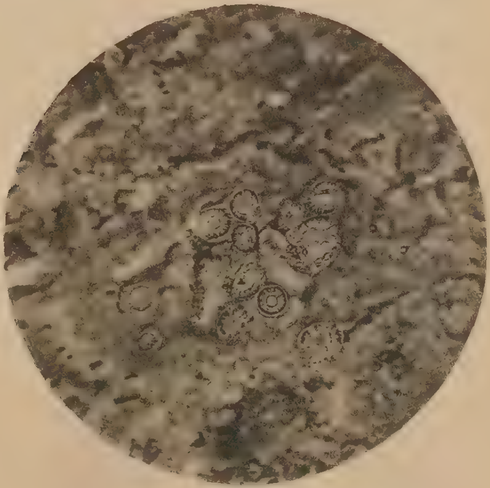
1.



2.



3.



4.

Photo. Russell C. Vernon.

John Bale, Sons & Curnow, L.td London.

VARIATIONS IN THE CHEMICAL COMPOSITION OF HERRING

By John Arnold Lovern, B.Sc., Ph.D.

The Torry Research Station, Aberdeen, of the Department of Scientific and Industrial Research

and Henry Wood, M.A., Ph.D.

The Marine Laboratory of the Fishery Board for Scotland, Aberdeen

(Text-figs. 1–2)

Of the three main components of the flesh of the herring—protein, fat and water—the last two vary widely with the time of the year, the habitat, and the condition of the fish. There are corresponding variations in the palatability, texture, food value and commercial value. The variations in protein are much smaller, and have no commercial significance.

Channon & Saby (1932) give a summary of earlier work showing that there is a rise in the fat content of herring muscle before spawning, followed by a fall to a minimum after spawning. These authors studied the fat variations in Manx herring, dealing with liver, mesentery and gonads as well as muscle.

In this study attention has been confined to the body fat, i.e. the fat which lies below the skin and between the muscles. The liver is a small organ of little or no significance as a depot for fat. The fat content of the gonads varies erratically, averaging about 3 %. The mesenteric fat constitutes a depot, but one of less importance than the body fat. It is quickly used up during the maturation of the gonads. During winter all herring, irrespective of the seasons at which they spawn, are in a lean condition. In April a perceptible increase takes place in the plankton, which normally becomes abundant in the north-western North Sea in May and June, and leads to a concentration of herring in this region. Throughout May and June the fish feed heavily, their stomachs being packed with food, or showing evidence of recent feeding. During this period fat is rapidly stored in the flesh and around the intestines. In July feeding becomes less intensive. This seems not to be associated entirely with the development of the gonads, for whether this development is taking place or not much less food is found in the stomachs than in those of fish caught in May and June.

Herring showing significant anatomical differences, corresponding with differences in the times of spawning, are held to be of different races. In the Scottish area two distinct races have been established, "spring-spawners", spawning in February and March, and "Scottish autumn-spawners", spawning in August and September. The herring of the Scottish Summer Herring Fishery include both these races, and also adults from two other stocks, viz. that which spawns near the Dogger Bank and off the coast of Lincolnshire in September and October and that which gives rise to the Lowestoft and Yarmouth fisheries in October and November and spawns at the eastern entrance to the English Channel in December and January.

In view of the mixed racial character of certain populations of herring and since different races do not spawn at the same season, it is desirable to follow the changes in composition in material biologically as uniform as possible.

Only reasonably fresh herring were used. In almost every sample the dominant groups as regards size and maturity were analysed. In some cases when two groups were present in a sample, whether judged by maturity or size, analyses were made of both. As a rule, however, maturity was regarded as the most important variable, and groups were so selected that analysis was made of herring at all stages from the immature to the spawning or spent condition. Maturity is expressed on the following scale, adopted by the International Council for the Exploration of the Sea:

STAGE I.	Sexual organs small; breadth about 2–3 mm.; clear wine or amber colour. No eggs visible to naked eye. (Immature.)
STAGE II.	Diameter nearly 1 cm.; length slightly more than half length of body cavity. Eggs small, unyolked, visible to naked eye. (Developing immatures and recovering spents.)
STAGE III.	Organs occupying about half of body cavity. Eggs amber coloured, yolked.
STAGE IV.	Organs filling about two-thirds of body cavity. No large transparent eggs.
STAGE V.	Organs filling body cavity. Some large transparent eggs may be present.
STAGE VI.	Spawning in progress or just imminent. Large transparent eggs.
STAGE VII.	Spent. Organs bloodshot. Large residual eggs present.

The analyses (determination of fat, solids and water contents) were carried out on samples consisting of fillets of six or more fish. Removal of the skin led to loss of fat, and in all samples after the first few the skin was left on. After mincing and thorough mixing, a weighed portion of the sample was dried at 105° C. until sufficiently dry for the fat to be extracted with ether. The residue was then returned to the oven and dried to constant weight, giving the "solids", mainly crude protein.

At first the sexes were examined separately. Table I shows that the variations are very similar in males and females. The maturing females seem to have a slightly lower fat content than the males in July and August, possibly associated with the maturation of the gonads, for in the final phase the ovaries appear to mature more rapidly than the testes. Subsequently the sexes were not separated, males and females being present in the samples in roughly equal proportions.

The greatest variations occur in the water and fat, which vary in inverse

TABLE I. CHEMICAL ANALYSIS OF MALE AND FEMALE HERRING FROM THE SCOTTISH NORTH-EAST COAST, 1935

	Males				Females			
Date	Maturity	Water %	Solids %	Fat %	Maturity	Water %	Solids %	Fat %
May 21	I	68·3	21·1	10·6	I	72·7	19·2	8·1
June 3	VII–II	69·2	19·0	11·8	VII–II	67·8	18·7	13·5
,, 5	I	73·6	20·1	6·3	I	72·0	19·8	8·2
	VII–II	72·0	19·3	8·7	II	72·7	19·5	7·8
,, 12	II+	62·0	19·2	18·8	II+	66·0	19·6	14·4
,, 18	II+	65·6	18·7	15·7	II+	66·2	18·8	15·0
,, 25	II+	64·6	18·7	16·7	II+	60·0	20·5	19·5
,, 25	II	*62·5	18·7	18·8	II	62·4	18·6	19·0
		66·2	19·2	14·6				
July 2	II+	†61·3	17·2	21·5	II+	60·4	18·1	21·5
,, 23	III–IV	57·5	20·2	22·3	III–IV	60·8	20·7	18·5
Aug. 14	IV–V	62·7	21·4	15·9	IV–V	65·3	20·9	13·8
,, 20	VII	70·6	18·5	10·9	VII	70·6	19·3	10·1
,, 27	V	65·6	18·2	16·2	IV–V	69·5	18·3	12·2
	VII	69·7	19·0	11·3	VII	68·9	19·6	11·5
Dec. 19	VII	76·8	21·0	2·2	VII	75·5	21·3	3·2

* With skin and without.

† This sample and others subsequent with skin on.

ratio. By comparison, the variations in the solids are slight, and appear to be independent of the variations between fat and water. In view of the reciprocal relation between fat and water, discussion may be limited to fat and solids.

FAT

Immature Herring

The proportions of the different stocks and races of herring in the population of the north-western North Sea vary from year to year and, within the same season, according to the grounds and time of year. The immature herring of the grounds between Shetland and Peterhead include, however, only the native stocks, i.e. Scottish spring and Scottish autumn spawners (Wood, 1936). The immature fish in the region of Shetland belong almost exclusively to spring-spawning stock. From Orkney southwards along the north-east and east coast, sexually immature fish of autumn-spawning stock come into prominence, and normally predominate in the Moray Firth and other shallow regions.

TABLE II. CHEMICAL ANALYSIS OF FLESH OF IMMATURE HERRING FROM THE NORTHERN AND NORTH-WESTERN NORTH SEA. STAGE I

Area	Date	Size range (cm.)	Age (years)	Water %	Solids %	Fat %
Shetland	1936 Apr. 9	25·7–26·9	3	74·8	19·7	5·5
	May 25	25·0–26·5	3¼	71·3	19·5	9·2
Scottish north-east coast	1935 May 21	21·8–23·5	3	70·5	20·2	9·3
	1936 June 2	22·7–23·9	3¾	62·8	19·2	18·0
	1935 June 5	20·5–22·7	3⅓	72·8	19·9	7·3
Berwick coast	June 11	21·0–22·4	3+	68·7	22·7	8·6
	July 23	20·9–22·2	2¾	64·5	19·6	15·9
Forth	1936 Jan. 14	18·0–20·7	2+	73·7	19·2	7·1
	1937 Feb. 16	17·8–21·1	2+	73·5	19·8	6·7
	Mar. 9	18·0–20·0	2+	75·7	19·1	5·2

Table II* shows that the lowest values for fat occur in March and April. Fat begins to accumulate in May and reaches its highest value in June and July. It will be seen later that the range of the values is not so great in immature as in adult herring. While the immature fish are able to maintain the higher reserve of fat over the winter, they do not appear to reach the same degree of fatness as adult herring during summer (Tables IV and V); Table II does not, however, include samples of immature herring from Shetland in June and July when they are normally "prime" fish and undoubtedly have a high fat content. Many of the immature fish caught off the Scottish east and north-east coasts in June and July remain immature for another year, and their comparatively rapid growth may not permit the accumulation of a reserve of fat equal to that of adult or nearly adult herring, which require much less food for growth.

---

* The average age of the fish is given in this and subsequent Tables, although there is no indication that age alone has any appreciable influence on the variations in herring of marketable size.

Table II also brings out the great variation in fat content from year to year and place to place. The highest values were recorded in the north-eastern area on June 2 1936, while a sample from the same fishing ground on June 5 1935 had the lowest value yet recorded in June.

The data hardly warrant a comparison between herring of the northern areas and those of the more southerly grounds off the Scottish east coast. The records available indicate that the former build up a reserve of fat more quickly than the latter. The differences in the values given in Table II cannot be regarded as constant but they are such as might be expected from the distribution of the organisms on which the herring feeds. These organisms, many of which are derived from regions beyond the North Sea, are patchy in their occurrence, but according to Gibbons (1936) and Gibbons & Fraser (1937) they are numerous in April and May in the neighbourhood of the Shetland and Orkney Islands, and in May and June are more numerous off the north-east coast of Scotland than off the east and south-east coasts.

Adult Herring of the Northern and North-western North Sea

Adult here means herring that have spawned and herring that have developed beyond the immature stage and are preparing to spawn at an early date. Examples given here may be accepted as typical of the adult herring caught in the drift-net. The first series of records (Table III) was obtained from catches in Shetland waters where spring-spawning and adult autumn-spawning herring sometimes occur together in dense shoals in April and May.

TABLE III. ANALYSIS OF ADULT HERRING: SHETLAND: APRIL-MAY. MATURITIES VII AND II. (RECOVERING SPENTS)

Date	Size range (cm.)	Age (years)	Water %	Solids %	Fat %
1935 Apr. 3	25·9–28·8	6	76·3	21·5	2·2
„ 17	25·0–28·8	6	77·5	19·5	3·0
„ 22	25·0–28·6	5¾	78·8	19·1	2·1
May 20	26·0–29·0	5½	76·1	20·1	3·8
1936 Apr. 9	27·8–30·0	6	79·1	19·9	1·0
„ 27	28·8–30·3	6+	78·9	19·9	1·2
May 1	27·0–29·2	6½	77·4	20·0	2·6
„ 23	26·0–28·1	6	73·9	19·3	6·8

The percentages of fat are uniformly low, and minimal values are reached in April. During April food normally begins to be abundant in this area, and gives rise to the great concentrations of herring in April and May. In May, when feeding has been going on for some weeks, an increase in the fat content becomes apparent.

The next series (Table IV) refers to adult herring caught off the north-east coast on the grounds normally fished from Wick, Fraserburgh and Peterhead.

TABLE IV. ANALYSIS OF ADULT HERRING. NORTH-WESTERN NORTH SEA

Date		Place of capture	Maturity	Size range (cm.)	Age (years)	Water %	Solids %	Fat %
1935 June	3	Scottish north-east coast	VII–II	23·8–27·7	5¼	68·5	18·8	12·7
,,	5	,,	,,	22·4–24·7	4	72·4	19·4	8·2
,,	12	,,	II+	23·5–24·7	3¾	64·0	19·4	16·6
,,	18	,,	,,	23·6–25·7	4¼	65·0	19·7	15·3
,,	25	,,	,,	24·0–25·6	3⅔	62·3	19·6	18·1
,,	25	,,	II	22·3–25·0	3⅔	63·7	18·9	17·4
July	2	,,	II+	23·8–26·1	4¾	60·9	17·7	21·4
,,	23	,,	III–IV	24·6–27·8	5	59·2	20·4	20·4
Aug.	14	,,	IV–V	—	7	64·0	21·2	14·8
,,	27	,,	IV–V	27·8–29·9	7¼	67·6	18·2	14·2
,,	20	,,	VII (spents)	24·7–30·5	7	70·6	18·9	10·5
,,	27	,,	,,	25·0–29·5	6	69·3	19·3	11·4
Oct.	28	Fladen*	,,	27·5–29·1	7+	72·6	19·4	8·0
Nov.	12	,,	,,	26·6–29·1	6½	73·4	19·5	7·1
,,	27	,,	,,	26·7–28·5	7½	74·9	20·1	5·0
Dec.	19	Scottish north-east coast	,,	25·2–26·5	3¾	76·1	21·2	2·7
1936 June	2	,,	II	24·0–24·9	4½+	63·4	19·5	17·1
July	14	,,	IV–V	26·0–30·0	5+	64·5	18·9	16·6
Nov.	30	Fladen*	VII	27·1–28·7	8¾	73·2	19·6	7·2

* *Vide infra.*

Most of the herring caught off the Scottish north-east coast in June are only at Stage II of maturity. During this month little development of the gonads takes place. There is, however, a rapid increase in the fat content, which reaches its highest value early in July. Thereafter development of the reproductive organs, accompanied by a gradual decline in the fat content, becomes evident. During the later stages in the maturation of the gonads little food is taken, so that the reserves of fat may not be used entirely to meet the demands of the reproductive system.

The analyses for the period July 23–December 19 1935, and for July 14 and November 30 1936, refer exclusively to Scottish autumn-spawners. During these periods the herring were considerably larger than those caught on the same grounds in June, and in this respect they resemble much more closely the samples obtained from Shetland waters in April and May (Table III).

Table IV shows that the fish which spawn near the Scottish east and north-east coast maintain a considerable reserve of fat for some time after spawning by a short period of intensive feeding in August and September. The effect of the decreasing supply of food is apparent in the gradually declining fat content of spent herring from the Fladen ground in October and November; that for December 19 1935, north-east coast, seems abnormally low.

The Herring of the Fladen Ground

The Fladen ground, a comparatively deep basin, approximately 100 miles east-north-east to north-east by east of Aberdeen and beyond the economic range of drifters, is one of the few where herring are caught at the bottom by trawl. The season commences as a rule in the last fortnight of July, and may extend until November or December. During this period important changes take place in the composition of the shoals. In July and August the catches consist mainly of the larger sizes of the stock or stocks which spawn in the late autumn in the area of the Dogger Bank and the southern North Sea, and probably include herring from the East Channel winter-spawning stock. These herring leave the Fladen ground in September for their spawning grounds. Before their departure is completed, herring of entirely different stocks appear, viz. spent fish of Scottish autumn-spawning stock and maturing spring-spawners, whose gonads are still small in September and October, the majority being only at Stages II and III of maturity. The spent fish have been included in Table IV.

Table V gives the analysis of herring that spawn in late autumn in the middle and south North Sea, caught, first, on the Fladen ground in July and August, and, later in the year, off the East Anglian coast.

TABLE V. ANALYSIS OF LATE AUTUMN AND (WINTER?) SPAWNING HERRING. FLADEN AND EAST ANGLIA

Date	Place of capture	Maturity	Size range (cm.)	Age (years)	Water %	Solids %	Fat %
1935 July 18	Fladen	II	24·8–26·7	4¾	60·3	18·0	21·7
Aug. 19	,,	IV–V	27·6–29·4	7+	66·4	17·7	15·9
1936 Oct. 6	Dogger	,,	27·0–29·0	—	68·3	18·0	13·7
1935 ,, 23	Off Lowestoft	,,	23·7–24·7	4	67·7	18·3	14·0
Nov. 13	,,	,,	26·6–28·7	7¾	67·6	18·3	14·1

Those caught on the Fladen ground in July at the earlier stages of sexual development have a high fat content. In August the more developed fish show a considerable decline, although fatter than herring of corresponding maturity caught at the same time on the drift-net grounds. Thus, this component of the Fladen population has a large store of fat on its departure to spawn in the middle and southern North Sea. The samples caught off Lowestoft show that the reserve may be maintained until October and November, provided that spawning has not taken place.

Spring-spawners are normally abundant between Shetland and the west coast of Norway in April and May, and around Shetland from May until about mid-July. From these sources come the spring-spawners which begin to assemble on the Fladen ground in September. Coming from an area where food is abundant in spring, they must have accumulated fat at least as fast as the fish of the June series in Table IV.

TABLE VI. ANALYSIS OF SPRING-SPAWNERS—FLADEN GROUND, CAITHNESS COAST AND FORTH

Date	Place of capture	Maturity	Size range (cm.)	Age (years)	Water %	Solids %	Fat %
1935 Oct. 28	Fladen	III	27·5–30·0	5	66·9	18·3	14·8
Dec. 11	,,	IV–V	27·2–29·6	5+	66·5	17·7	15·8
Feb. 14	Caithness coast	,,	27·0–28·0	4	73·3	18·9	7·8
,, 13	Forth	VI	—	—	77·0	19·8	3·2
,, 26	,,	VII	25·3–29·0	5	76·4	19·4	4·2
Mar. 11	,,	VI	26·3–34·2	6¾	78·2	18·6	3·2
,, 25	,,	VII	26·4–30·2	4+	78·3	19·8	1·9
1936 Jan. 14	,,	III–IV	22·3–23·9	3+	69·8	18·9	11·3
Feb. 4	,,	,,	25·7–27·3	4¾	71·1	19·9	9·0
,, 25	,,	VI	27·1–28·3	6	75·5	18·8	5·7
Mar. 10	,,	,,	27·1–28·8	4⅔	76·9	19·9	3·2
,, 24	,,	,,	26·9–28·7	5−	76·8	18·9	4·3
1937 Feb. 16	,,	,,	22·3–23·9	3+	73·0	19·1	7·9

Table VI refers only to spring-spawning herring, although it is not implied that all belong to the same spawning community. Racial analysis was carried out on all samples, and evidence was found that the sample of February 14 1935 from the Caithness coast and the sample of March 25 1935 from the Forth were identical with the spring-spawners from the Fladen ground the previous autumn. The series gives some indication of the rate at which the reserves of fat are expended. The maturing spring-spawners caught on the Fladen ground in October and December have values ranging from 14·8 to 15·8 %. A sample of maturing herring (maturity III–IV) from the Forth, caught on January 14 1936, gives a relatively high value of 11·3 %, and another sample of the same maturity, caught on February 4, gives a value of 9·0 %. A sample at Stage IV, obtained in February 1937, gives a value of 7·9 %, while the figure for that from the Caithness coast, which was slightly more mature, is 7·8 %. Apart from these relatively high values, the other samples caught in February and March, and consisting of spawning or spent fish, give low values ranging from 1·9 to 5·7 %. Thus, there is a fairly rapid decline in the fat content, corresponding with the rapid final phase in the development of the gonads.

Tables V and VI make it clear that all the herring, other than spent fish, caught in autumn and late autumn on the Fladen ground, have a high fat content which is fairly well maintained until a short time before spawning.

Clyde Spring-spawners

In recent years the summer and autumn catches within the Clyde estuary have consisted almost exclusively of small immature herring or herring maturing for the first time. On the other hand, the spawning shoals caught in spring are extremely variable in size and age, including small fish from the estuary and older and much larger fish from sources outside the estuary. The data for this region are given in Table VII.

TABLE VII. ANALYSIS OF CLYDE HERRING

Date	Maturity	Size range (cm.)	Age (years)	Water %	Solids %	Fat %
1935 Feb. 7	V	?	?	75·2	18·9	5·9
„ 7	V–VI	25·5–31·9	?	76·5	19·8	3·7
Mar. 6	VI	26·7–28·9	4	78·3	18·8	2·9
July 3	I	20·6–22·3	2¼	59·4	20·0	20·6
Sept. 5	„	19·8–21·2	2½	59·2	20·4	20·4
„ 5	II–III	22·9–24·3	2½	60·0	21·2	18·8
1936 Jan. 21	III–IV	22·3–24·9	2¾	69·6	18·0	12·4
Feb. 4	„	23·1–24·7	3 –	72·0	18·4	9·6
„ 12	V–VI	28·0–29·8	4	71·9	19·7	8·4
Mar. 16	VI	23·3–24·7	3	76·1	18·8	5·1

When spawning is completed in February and March, the spent shoals leave the estuary and rarely return until the approach of the next spawning. Thus, it is impossible to observe the rate at which the spent adults recover. In spite of the lack of records between March and July, it is apparent that the Clyde herring accumulate fat rapidly during early summer. The high figure of 20·6% recorded on July 3 is maintained until September, when a slight decline is seen in herring whose gonads have begun to develop. Few of the estuarine stock reach Stage IV of maturity before January, so that there is every reason to believe that the reserves of fat are well maintained until the end of the year. In January and February, with the acceleration in maturation and a declining supply of food, the stored fat begins to be used up, and at the spawning season reaches low values, which, however, are rarely so low as in the spring-spawning herring of the Forth.

Northern North Sea Spring-spawners

During winter, more particularly in February and March, shoals of large herring concentrate along the continental slope, and are frequently caught by trawlers in the region of the Viking Bank, a few miles off the north and north-west coasts of Shetland and in the neighbourhood of the Flannan Islands, which lie in the Atlantic to the west of Lewis. These herring differ in important respects from North Sea herring. As a rule they are larger and older, and are rarely found near the coasts until spawning time. The analysis of the few samples examined is given in Table VIII.

TABLE VIII. ANALYSIS OF ADULT HERRING OF THE ATLANTIC SLOPE

Date	Place of capture	Maturity	Size range (cm.)	Age (years)	Water %	Solids %	Fat %
1935 Mar. 12	Shetland	VI	32·5–35·9	12	74·4	17·7	7·9
„ 12	„	VII	30·9–37·2	8	74·0	18·4	7·6
1936 Feb. 25	„	V–VI	33·4–35·2	11¼	63·1	17·3	14·6
1937 Feb. 18	„	IV–V	32·9–34·5	9½	68·7	18·7	12·6
Apr. 20	North Ireland	VII	32·5–33·9	7	75·5	20·0	4·5

The series in Table VIII has the highest values for fat yet recorded in February and March. Some loss may be expected before food is available in abundance in April and May*; the sample from the north coast of Ireland on April 20, 1937 gives a value of 4·5%. Nevertheless, it appears that the reserves of these herring are not so severely taxed during winter as those of the smaller North Sea stocks.

Fig. 1 gives the approximate fat content of the chief North Sea stocks throughout the greater part of the year. It is assumed that fat accumulates more or less uniformly in all stocks in May and June. How long a high fat content is retained after the maximum has been reached in July largely depends on when spawning takes place. The breaks in the curves, joined by dotted lines, require explanation. At these periods both spawning (or ripe) and spent fish occurred in the catches. The spawning fish gave the higher values and the spent fish the lower. After these periods only spent fish were obtained. There is evidently a rapid loss of fat during spawning.

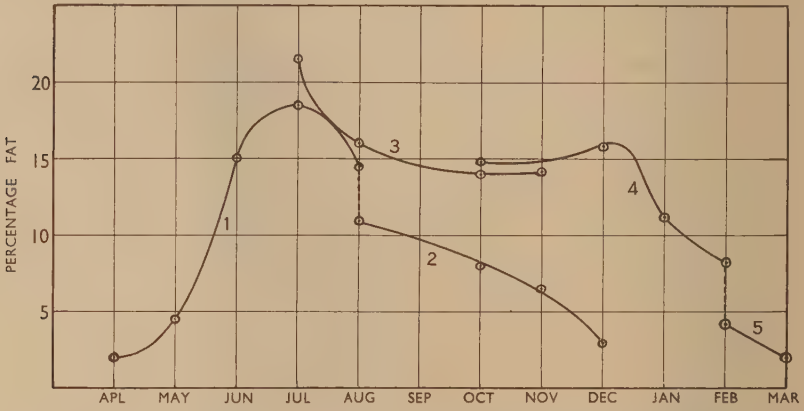


Fig. 1. Fat content of North Sea herring (adult stages). 1, Scottish autumn spawners; 2, Scottish autumn spents; 3, middle and southern North Sea spawners; 4, Scottish spring spawners; 5, Scottish spring spents.

SOLIDS

The range in the percentage of solids recorded here is from 17·3 to 22·7; the variation recorded by one of us (J. A. L.) for a greater number of samples (131) is from 16·1 to 22·7. In Fig. 2 the percentages found in these 131 samples are plotted against the frequency (number of samples) of their occurrence. The range 18–20% covers most of the samples.

Variations in the solids content must almost certainly be ascribed to variations in protein content, since no other constituent of the solids is present in a sufficiently large proportion to account for them. The protein in fish can vary with the intensity of protein feeding, as shown by McCay & Tunison (1936) for trout; the variations they induced experimentally were of about the same order as those found in the solids of the herring.

---

* Table III shows that the lowest values occur in April.

If the variations in herring are due to differences in intensity of feeding, a high solids content should appear at about the same time as the maximal fat content. Further, minimal values for solids would be expected in ripening fish, which as a rule take little food, and still more so in spent fish.* In the Clyde herring such a relationship is apparent. The highest values for this region were found in young fish, caught in July and September, which were either immature or beginning to mature for the first time. The values during or immediately prior to the spawning were relatively low.

Table IV shows, however, that the solids may have a high value in both maturing and spent fish. In fact, it might appear from the tables as a whole that the solids vary erratically. Actually, the variations are probably the net result of several factors, including the feeding and spawning cycles. Race, however, appears to be at least equally important. For example, Table V shows that the herring which spawn in the middle or southern North Sea in the late autumn or winter have relatively low values for solids, as have also the samples caught off Lowestoft in October and November. Moreover, Table VI shows that the spring-spawners caught on the Fladen ground in October and December show relatively low values. These spring-spawners have been identified with the Shetland spring-spawners (Wood, 1937), and Table VIII shows that the large oceanic spring-spawners caught in the neighbourhood of the Viking Bank and off Shetland show the lowest values for solids of all the series detailed. By comparison the spring-spawners of the Firth of Clyde and those caught off the north-west of Ireland in April 1937

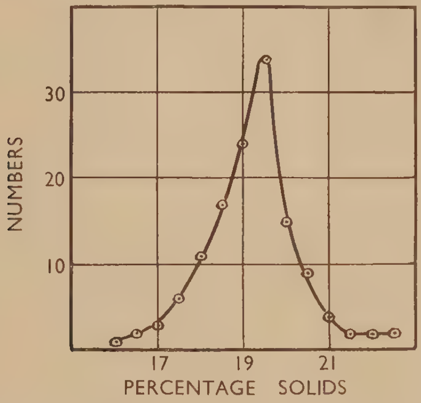


Fig. 2. Frequencies of solids contents (%) in herring fillets.

---

* Especially in view of the large quantities of protein transferred to the maturing gonads.

show significantly higher values. The herring from the Scottish north-east coast (Table IV) show a relatively wide range in the solids, which cannot be explained entirely by the mixed composition of the population. The very low value obtained for the sample of July 2 1935 suggests that it belonged either to Shetland spring-spawning or middle or southern North Sea spawning stocks, rather than to Scottish autumn-spawning stock; racial analysis definitely ruled out the possibility of it being of Shetland spring-spawning stock, and indicated that the racial characters were nearer to Dogger Bank or middle North Sea spawning stock than to Scottish autumn-spawners.

The smooth shape of the curve in Fig. 2, and the absence of more than one maximum, suggests that racial peculiarities in the solids content cannot be sharply defined and must overlap considerably. This is, perhaps, what would be expected by analogy with other racial characteristics. The masking effect of the spawning and feeding cycles must also be borne in mind.

It is inadvisable as yet to draw any further conclusions from the variations in solids contents; more detailed investigations are necessary for the elucidation of their causes.

SUMMARY

A study has been made of the seasonal and other variations in the contents of fat, water and total solids (other than fat) of the flesh of herring. The herring studied were mainly from Scottish and Shetland waters.

Various races of herring, differing anatomically and with different spawning seasons, are considered separately. For each, the observed changes in chemical composition are considered in relation to the season of the year and the feeding and spawning cycles of the fish.

During May and June there is a rapid rise in the fat content of herring (demonstrated for some races and inferred for the rest). This is correlated with a period of intensive feeding. After the attainment of maximal values in July there is a fall to minimal values in April. The rapidity of the fall depends on the spawning season, a relatively high fat content being maintained until spawning takes place. During spawning there is a rapid fall in the fat content, due, in part at least, to cessation of feeding.

The variations in the solids content of herring are of a smaller order. The causes of them are not clear, but probably several factors are involved, including the feeding and spawning cycles and race.

The water content varies inversely with the fat content, and is not separately considered.

REFERENCES

CHANNON, H. J. & SABY, M. K. E., 1932. Fat metabolism of the herring. I. A preliminary survey. *Biochem. Journ.*, Vol. 26, pp. 2021–34.

GIBBONS, S. G., 1936. *Calanus finmarchicus* and other copepods in Scottish waters in 1933. *Fisheries, Scotland, Sci. Invest.*, No. 2.

GIBBONS, S. G. & FRASER, J. H., 1937. Experiments with the "Hardy" plankton indicator in Scottish waters. I. *Journ. Cons. Int. Expl. Mer*, Vol. XII, pp. 45–50.

McCAY, C. M. & TUNISON, A. V., 1936. *Cortland Hatchery Report*, No. 5. (N.Y. State Cons. Dept., U.S. Bur. of Fish. and Cornell Univ.)

WOOD, H., 1936. Race investigations of the herring population of Scottish waters. *Fisheries, Scotland, Sci. Invest.*, No. 3.

—— 1937. Movements of herring in the northern North Sea. *Fisheries, Scotland, Sci. Invest.*, No. 3.

THE PRESERVATION OF CONTRACTILE MARINE ANIMALS IN AN EXPANDED CONDITION

By H. A. F. Gohar, M.Sc., Cairo

The importance of killing contractile animals in an expanded condition cannot be over-estimated. A glance at the immense confusion and uncertainty which prevails in several branches of tropical marine invertebrates, and in particular the Coelenterata, will give a clear picture of the value of good preservation. Killing contractile animals in an expanded condition has always offered considerable difficulty. Several methods have been recommended for different animals, but it is often very difficult to choose the appropriate one, since animals belonging to one and the same group may behave quite differently towards any method. The writer, during his work for the last three years at the Marine Biological Station of the University of Cairo at Ghardaqa* in the Red Sea, has taken great pains to preserve a variety of marine invertebrates as fully expanded as possible. Some of the successful results and the methods used are therefore given here.

The commonest method for the present purpose is the use of narcotics. The most familiar of these are menthol, chloral hydrate, alcohol, magnesium sulphate and cocaine. Owing to the difficulty in obtaining cocaine it cannot be freely used for general purposes. Menthol enjoys a great reputation for narcotization which, in fact, it does not quite deserve. Although in some few cases it gave good results, yet in the majority it was quite unsatisfactory, as delicate animals begin to macerate before they are properly narcotized. It is generally applied in the crystal form and sprinkled on the surface of the water. Apparently its low solubility is responsible for a great many of its failures. This difficulty of solution was sometimes overcome by using an alcoholic solution of menthol and spreading it on the surface of the water. Better results were obtained in this way with some nudibranchs and alcyonarians.

Chloral hydrate and alcohol were used for various animals but with little success. Chloroform vapours were useful in killing crabs without breaking their legs.

Magnesium sulphate is the most popular of all narcotics for marine animals, and in fact it deserves its popularity, as it gives satisfactory results with a great variety of animals. It is, however, essential that the animal to be narcotized should be put in plenty of clean sea water and the salt be added gradually at intervals of about 10 min. or so. The time required for complete narcotization

* Hurghada on charts.

differs with the kind and size of the animals, but is generally between 5 and 24 hours. It is best to put the narcotic in a corner of the vessel farthest from the animal. To avoid fractional addition of magnesium sulphate the required quantity may be packed up in a bag of fine-meshed gauze and the latter put into the vessel containing the animals to be narcotized, also at a corner farthest from the animals.

By this method the giant nudibranchs, *Hexabranchus sanguineus*, *Thordisa crosslandi* and *Asteronotus hemprichi*, also *Doridopsis nigra*, *Pleurobranchus delicatus*, the pulmonate *Oncidium* sp., the placophores *Acanthochiton spinigera* and other chitons were successfully killed. Among the Madreporaria, *Goniopora columna*—which is fully expanded in the sea in full sunlight—*Fungia* sp., *Turbinaria mesentrina*, *Favia* sp. and others give satisfactory results after narcotization with magnesium sulphate.

Planarians are usually successfully killed by hot sublimate solution without previous narcotization. Sometimes, however, it is desirable to avoid the use of sublimate. They can easily be narcotized with magnesium sulphate, spread on a glass slide and killed with whatever fixative may be required.

Of the Alcyonaria, *Tubipora musica*, *Acabaria pulchra* (Hickson, 1937), *Clathraria rubinoides*, four species of *Sympodium* and two species of *Clavularia*, all of which are completely retractile, lend themselves easily to this method of narcotization. It is of very little value, if any at all, with other alcyonarians such as all species of the genera *Alcyonium*, *Sarcophytum*, *Lobophytum*, *Sinularia*, *Dendronephthya* and others. The animals never remain fully expanded after the addition of the narcotic, and, moreover, they usually macerate before they are sufficiently narcotized.

There is, however, one drawback to the use of this method, and this is that a great amount of the salt has to be used—about 150 g. or more per litre of sea water. The great osmotic pressure it develops and the very long time through which it has to act are liable to make major changes in the delicate structures of the tissues, thus rendering animals killed by this method of little value for cytological or even histological purposes.

Another method, which proved quite satisfactory and at the same time has not the drawbacks mentioned above, was, as far as the writer is aware, used here for the first time. This is accomplished by killing the animals gradually and insensibly by formalin. The method is summarized as follows. The animal is put in a great bulk of sea water 50–500 times its volume or more. After it has properly expanded a few drops of dilute formalin are added (3 drops of 1 % formaldehyde to 100 c.c.), and this is repeated at intervals of about 15 min. The amount of formalin added may be doubled every hour. The animal eventually dies with but very little or no contraction.

Two species of *Aeolis* have defied every other method. The cerata fall off at the slightest disturbance, even the transfer from one aquarium to another is quite sufficient to cause the withering of some cerata. All sorts of narcotics have the same effect. These two species of *Aeolis* lend themselves to the gradual action of formalin in a remarkable manner and are killed in a perfect condition. The only other method to which these two aeolids yield is freezing and thawing the frozen mass in strong formalin, as will be mentioned below.

Other examples of animals that yield to the gradual poisoning by formalin are *Hexabranchus sanguineus*, *Doridopsis nigra*, *Oncidium* sp., *Acanthochiton spinigera*, *Acabaria pulchra*, *Sympodium coeruleum*, etc. The ophiuroid *Astroboa* sp. also yields to this method, but this animal should be left to expand in a flat dish and the excess of water siphoned off, leaving just enough to cover the animal; the formalin is then applied.

Some animals, such as the anemones *Actinia quadricolor* and *Thalassianthus aster*, are extremely sensitive to great dilutions of formalin and at the same time could not readily be sufficiently fully anaesthetized by any narcotic. These, however, respond well to partial narcotization with magnesium sulphate together with the treatment with formalin described above. The magnesium sulphate thus reduces the sensitivity of the animals to the gradual poisoning by formalin.

Narcotization by freezing seems to be a very promising method and deserves some effort towards its development and the generalization of its use. It has the advantage that animals are not liable to any maceration during the process, and accordingly the finer structures of the tissues are likely to be better preserved than by any other method. The effect of low temperatures on marine animals is a point of extreme interest and importance, but unfortunately till now has not been thoroughly worked out. It is very probable that better knowledge of the temperature relations of these animals may give the clue to the successful killing of a great variety of marine invertebrates in an expanded condition. Preliminary attempts in this respect give us much hope. Many animals—some of them defy all other methods—are very successfully killed after freezing. The animals are put in plenty of clean sea water in a glass vessel. The latter is in its turn put into an ice chest till the water becomes ice cold; it is then transferred to a freezing mixture and left to freeze. After some time the frozen mass is taken out of the freezing mixture, and as much of the ice as possible is allowed to melt away without exposing the animals. The latter, embedded in just enough ice, are thrown into a strong fixation solution, e.g. fairly strong formalin, where the ice is allowed to thaw. By this method the two species of *Aeolis*—which yield only to gradual poisoning by formalin—are killed in the most perfect condition. *Glossodoris quadricolor*, *Chromodoris annulata*, several tritonid species and many other nudibranchs are killed in such an expanded condition unparalleled by any obtained by other methods. Some actinians, particularly small and moderately sized ones, were well expanded after preservation. In many cases lowering the water temperature even to freezing-point does not seem to be sufficient, as some animals seem to resist this temperature. They will move as soon as the temperature rises, and if killed at such low temperatures they will still shrink. Animals kept on ice overnight contracted when put into the fixative next morning. Freezing is, therefore, evidently essential, at least for some animals. It may be that freezing mechanically prevents the contraction of the animals on the application of the fixative, as the latter will act on any part of the animal immediately it is exposed, while the rest will be held by the frozen mass. It may be remarked here that the resistance of some of these tropical animals to low temperatures is surprising.

A method which proved very useful in killing a large variety of marine animals and which possesses the advantage of rapidity is the instantaneous killing by using boiling strong formalin. Hot fixatives have been used for killing animals that contract slowly, but even then the way they are used is bound to induce a certain amount of contraction in the process of removing the animals from the water and dropping them into the fixative. Here it is the fixative that is poured on the animals. The latter are put in a vessel just large enough to allow them to expand freely. The vessel ought to be about three times as high as the animals. The whole vessel may then either be put into a large aquarium with running sea water or the water be directly run into it according to the nature of the animals. When the animals have completely expanded, the vessel is removed very carefully from the aquarium or the running water stopped. The water in the vessel is very carefully run out by means of a siphon, without causing any disturbance to the animals, until just enough is left to cover the animals completely. A sufficient volume of concentrated formaldehyde solution (one-third to one-half the volume of the water containing the animals to be killed) at the boiling-point is now rapidly poured into the vessel. The animals are thus instantaneously killed without having any time to contract. They are then removed as rapidly as possible to the required preservative.

By this method the anemone *Thalassianthus aster* and the colonial anemones *Palythoa tuberculata* and *Palythoa* sp. were killed in a most perfectly expanded condition. Several other small anemones gave very good results. It always, however, failed with *Calliactis polypus* (commensal anemones with the hermit crab *Pagurus tinctor*) and the large anemones *Discosoma giganteum*, *Actinia quadricolor*, *Paractis adherens*, *P. hemprichi* and others. Among the Madreporaria *Fungia* sp. and *Goniopora columna* are killed in this way with little contraction. For the Alcyonaria, however, no other method compares with this. *Alcyonium*, *Sarcophytum*, *Lobophytum*, two species of *Clavularia*, four species of *Sympodium*, *Acabaria pulchra* (Hickson, 1937), *Acabaria* sp., *Tubipora musica*, and also hydroids, all give strikingly good results.

The majority of the nudibranchs do not lend themselves to this method, and all those tried contracted very badly on the addition of boiling formalin.

The use of boiling concentrated formalin has, unfortunately, the great disadvantage of being extremely irritating, and considerable care has to be taken in the manipulations. The formalin has to be boiled in a narrow-mouthed flask stoppered with cotton-wool. When the formalin is poured on to the animals, splashing ought to be carefully avoided as it seriously affects the skin. Its vapours are also injurious to the eyes, lungs and the mucous membranes of the respiratory system, so that the process may, at best, be carried out in a fume cupboard or, lacking that, a simple device may be used in its place. It is also strongly recommended that the worker should move to the open air immediately he pours the formalin on the animals.

In all the methods described above it is of prime importance that the animals should be fully expanded before the addition of the narcotic or preservative. Contracted animals are, in the overwhelming majority of cases, quite unlikely to expand under the effect of the narcotic. Some animals will not even expand if left in stagnant clean water: running water has to be used. It is therefore inadvisable to put the animals into the narcotizing or fixing solution, the narcotic or fixative has to be added to the water containing the animals. Narcotics or small doses of poisons are to be added very gradually so that the animals may be insensibly narcotized or poisoned. If such animals show any signs of contraction during the process, further addition of the narcotic should be stopped and the animals left undisturbed till they re-expand. Sometimes it is necessary that the narcotic in the water containing the animals should be diluted by the addition of more fresh sea water, or, the animals may even have to be removed to fresh sea water; then narcotization should be resumed after they have revived completely.

Animals that expand at night should naturally be dealt with at night.

REFERENCE

Hickson, S. J., 1937. The Family Melitodidae. *Trans. Zool. Soc.*, Vol. xxiii, p. 170.

OXYGEN PRODUCTION BY THE DIATOM *COSCINODISCUS EXCENTRICUS* EHR. IN RELATION TO SUBMARINE ILLUMINATION IN THE ENGLISH CHANNEL

By Penelope M. Jenkin, M.A.

Department of Zoology, Bristol University

(Text-figs. 1–9)

CONTENTS

	PAGE
Introduction	302
Method of Computing the Energy in Submarine Illumination	303
Measurement of the illumination in air	304
Measurement of the illumination in water	305
Assessment of the energy in the illumination	306
Apparatus and Methods for Measuring Illumination	307
Standards	307
Illumination integral	307
Extinction coefficients	309
Surface loss	310
Material and Methods for Measuring Photosynthesis	311
Choice of diatoms	311
Growth of cultures	311
Sterility of the cultures	312
Exposure of the diatoms in the sea	313
Estimation of oxygen	315
Calculating and recording the results	316
Accuracy of methods used in estimating photosynthesis	317
Factors Influencing the Rate of Photosynthesis during the Exposures at Sea	318
External factors	318
Internal factors	319
Results of the Experiments	323
Three short exposures in 1933	323
Successive four-hour exposures in 1934	325
Night exposure in 1934	326
Twenty-four-hour exposures in 1934	328
The Relation of Photosynthesis to Energy in the Sea	331
Acknowledgements	339
Summary	340
References	340
Appendix: Determinations of the Phosphorus and Nitrogen in *Coscinodiscus excentricus* Ehr. By L. H. N. Cooper	342

INTRODUCTION

Much attention has been directed in recent years to the analysis of the productivity of the sea. One of the most fundamental processes to be considered is the photosynthesis of marine plants, whereby the inorganic is converted to the organic by means of the energy in daylight.

Until the autumn of 1932 the measurement of photosynthesis and of light in the open sea had apparently only been measured independently, the former notably by Marshall & Orr (1928, p. 321), and the latter by Poole & Atkins (1926, p. 177, etc.).

The correlation of the two kinds of measurements appeared to be the next step; and, since the measurement of light is a more rapid process than that of photosynthesis, it was hoped that the establishment of any simple correlation might lead to more rapid means of assessing the possible productivity of natural waters. Measurements of photosynthesis were accordingly made by Marshall & Orr's method, with the co-operation of Dr W. R. G. Atkins, F.R.S., for the simultaneous measurements of light.

In 1934 a preliminary report by Pettersson, Höglund & Landberg (1934, p. 3), showed that they had undertaken a project rather similar to mine at almost the same time. Their results form a most interesting counterpart to mine, for in both cases the illumination was measured as well as the photosynthesis; but my aim was to expose diatoms at a set of constant depths and measure the variations in the illumination, while theirs was to expose mixed plankton samples to a constant illumination by varying the depth of suspension in such a way as to counterbalance the changes in daylight. Their method is ingenious but makes no allowance for the inevitable variations in the spectral composition of light that occur with change in depth of the water. Moreover, their plankton (Pettersson *et al.* 1934, p. 9) consisted of a mixture of different species of plants and even some animals, so that their results are more difficult to interpret than those obtained by using a pure culture of diatoms. This difficulty is also apparent in the methods adopted by most previous workers, except Marshall & Orr, for estimating photosynthesis (e.g. Gaarder & Gran, 1927, p. 8; Steemann Nielsen, 1932, p. 5, etc.). It was therefore considered a sufficient reason for spending much time and labour in growing cultures of the diatom *Coscinodiscus excentricus* Ehr. for use in the present investigation.

The oxygen production of these cultures was measured as an index of their photosynthesis, in preference to the carbon dioxide consumption, simply because of the ease with which oxygen in sea water may be measured by the Winkler method.

All the measurements of light, both in air and in the sea, were made for me by Dr Atkins, to whom, in conjunction with Dr H. H. Poole, I am also indebted for the following method of computing the energy in submarine illumination.

METHOD OF COMPUTING THE ENERGY IN SUBMARINE ILLUMINATION

The first difficulty in measuring submarine illumination is introduced by the changing spectral composition of the light that accompanies increasing depth below the surface. This is due to the differential absorption, or rather extinction, of light of different wave-lengths by the water. In air, measurements of the change in intensity of the light in one region of the spectrum are closely proportional to changes in intensity in the whole spectrum: under water, the proportionality is rapidly lost as the depth increases, because the intensity in each part of the spectrum decreases at an independent rate. Thus in clear water, for example, the light becomes not only fainter but much bluer, as it descends.

It is apparent that it is not correct to express submarine illumination in terms of the "lux" or metre-candle, nor is it convenient as the visual scale is not necessarily the same as the photo-electric, and the differential extinction of the spectrum under water alters the ratio of the one scale to the other.

The illumination in different submarine situations can therefore only be satisfactorily expressed and compared in terms of energy, if the comparison is to be valid, irrespective of the wave-lengths of the radiation.

Neither light nor energy, however, could be measured directly under water; but the work of Atkins & Poole (1936*b*, p. 1), on the luminous efficiency of daylight, and the standardization of photo-electric cells for the measurement of energy (Poole & Atkins, 1936, p. 363), allowed the energy to be computed indirectly, with a reasonable degree of accuracy.

Since the illumination to be dealt with is all submarine, it is possible to limit the radiant energy, which need be measured, to that within the visible spectrum (3800–7200 A.). The energy in the ultra-violet (wave-lengths shorter than 3800) is so rapidly absorbed by the sea, and forms, in any case, so small a proportion of the total energy in daylight, that its effect upon photosynthesis may be neglected (Spoehr, 1926, p. 117); while the energy in the deep red and infra-red (wave-lengths longer than 7200) is also absorbed very rapidly, and is so unlikely to effect any photosynthesis directly, that it may also be neglected. Moreover, any inaccuracy due to these assumptions would only affect the uppermost layers of the sea, where it is in any case difficult to obtain accurate measurements of either light or photosynthesis under ordinary seagoing conditions in the Channel.

Within the visible spectrum it seems probable that diatoms may make use of energy for photosynthesis almost equally in radiation of all wave-lengths (Stanbury, 1931, p. 651). This appears to hold good in spite of the heavier absorption shown by chlorophyll in certain restricted bands of the spectrum, particularly in the red region; it is possible that the accessory pigments in the diatoms may be responsible for absorbing the energy in other regions of the spectrum (p. 332).

It is therefore assumed, as a working hypothesis for the present research, that the total energy in all wave-lengths within the visible spectrum gives the best measure of the energy available for diatom photosynthesis in the sea.

Table I shows the method of computing the total energy at a series of depths, from the data obtained on August 28 1933. Values for light of different wave-lengths and the total energy on August 4 1933, are shown graphically in Fig. 1.

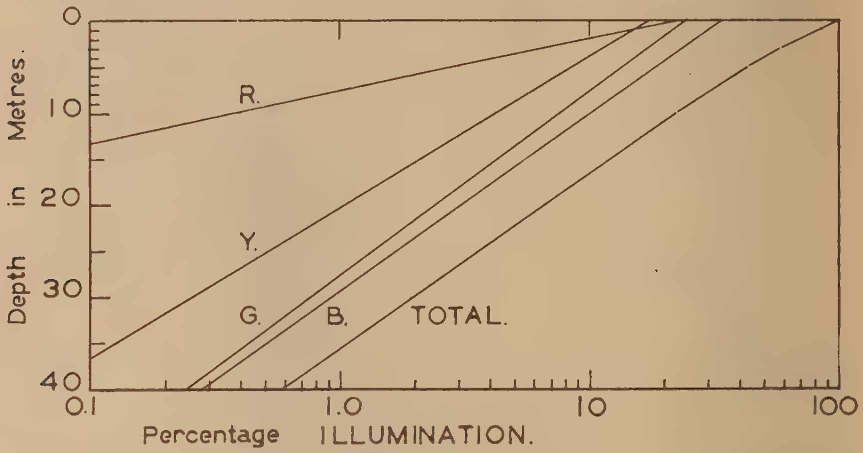


Fig. 1. Submarine illumination on August 4 1933. The percentages are given on a logarithmic scale. If 100% represents the subsurface daylight, the relative distribution of energy in air between "blue" 3800–4900 A., "green" 4900–5600 A., "yellow" 5600–6200 A., and "red" 6200–7200 A., is shown by the respective starting points of the lines *B*, *G*, *Y*, and *R*, at the surface (cf. Table II, column 5). The slope of these lines is determined by the extinction coëfficients. The curve on the extreme right shows the total illumination percentages.

The computation is made in a series of steps:

(i) *Measurement of the Illumination in Air*

The intensity of light in air is measured photo-electrically and expressed in lux.

The amount of light falling on a horizontal surface in air in a given time is the product of the intensity and the time; it has been called the "vertical illumination integral" (Atkins & Poole, 1936*a*, p. 257), and is measured in kilolux-hours. To allow for the varying intensity of daylight from hour to hour, and even from minute to minute, the intensity is recorded automatically every minute on a graph; the illumination integral is then obtained from the area enclosed on the graph, by the curve for intensity values and the time axis.

(ii) *Measurement of the Illumination in Water*

When light passes into water, the rays of different wave-length are extinguished at varying rates, owing to differential absorption, scattering, and other effects. Ideally, therefore, the rate of extinction for each wave-length should be measured separately: in practice a satisfactory degree of uniformity is achieved by measuring the rates for wave-lengths in four consecutive groups, namely "blue" 3800–4900 A., "green" 4900–5600 A., "yellow" 5600–6200 A. (measured by difference) and "red" 6200–7200 A. (*B*, *G*, *Y*, and *R*, Fig. 1). Colour filters were combined with photo-electric cells to measure the intensity of submarine light within each of the spectral regions, at a series of depths (Atkins & Poole, 1933, p. 134). The results were expressed as percentages of the intensity of subsurface light in the same spectral region (illumination percentages Table I and Fig. 1).

In water of uniform transparency, these illumination percentages decrease exponentially with depth, so that the rate of decrease, or extinction, can be expressed as a coefficient (extinction coefficients, Table I), which can then be used to calculate the percentages at intermediate depths.

TABLE I. COMPUTATION OF ENERGY IN SUBMARINE ILLUMINATION, ON AUGUST 28 1933

Exposure from 1140 to 1650 G.M.T. = 5·17 hr.
Vertical illumination integral in air = 201 kl.-hr.
Subsurface illumination (subtracting 15 % for reflexion) = 171 kl.-hr.
Derived subsurface energy integral = 256·5 joules or 61·6 g.-cal.
Factors for weighted energy percentage as for "sun and cloud" (see Table II, column 3).
Vertical extinction coefficients, blue 0·14, green 0·13, yellow 0·16, red 0·46, uniformly down to 30 m. (see Table III, p. 308).

Depth in m. ...	0		1		5		10		20		30	
Blue:												
Illumination %	100	—	86·9	—	49·5	—	24·4	—	6·1	—	1·5	—
Weighted energy %	—	26·7	—	23·2	—	13·2	—	6·5	—	1·6	—	0·4
Green:												
Illumination %	100	—	87·8	—	52·2	—	27·3	—	7·4	—	2·0	—
Weighted energy %	—	24·2	—	21·3	—	12·6	—	6·7	—	1·8	—	0·5
Yellow:												
Illumination %	100	—	85·2	—	44·9	—	20·2	—	4·1	—	0·8	—
Weighted energy %	—	19·7	—	16·8	—	8·8	—	4·0	—	0·8	—	0·15
Red:												
Illumination %	100	—	63·0	—	9·9	—	1·0	—	0·0	—	0·0	—
Weighted energy %	—	29·4	—	18·5	—	2·9	—	0·3	—	0·0	—	0·0
Total Weighted energy %	—	100·0	—	79·8	—	37·6	—	17·5	—	4·2	—	1·05
Energy Integral in Joules	—	256·5	—	204·6	—	96·5	—	44·8	—	10·8	—	2·7

(iii) *Assessment of Energy in the Illumination*

To convert the measurements of illumination into terms of energy it is necessary to know two more factors: the total amount of energy within the visible spectrum, represented by the illumination integral, for the daylight in air; and the distribution of that energy between the four spectral regions.

The distribution is derived from Abbot's curve (quoted by the International Congress of Photography, 1929, p. 152) for the relative energy distribution in mean-noon sunlight (Table II, column 3). These values were modified on most days, to allow for sky light being bluer than sunlight, the factors for weighting being derived from values given by Walsh (1928, p. 88), and Atkins & Poole (1931*a*, p. 34), as shown in Table II, column 4. The proportion of sunlight to sky light on the days of the experiments was usually taken as two to one, on the basis of Atkins & Poole's (1936*a*, p. 260) determinations; this gave the relative energy distribution shown in Table II, column 5 and applies to Fig. 1. Once, on August 28 1933, when the daylight was a mixture of bright sunlight and of light reflected from white clouds with no clear blue sky, the distribution of energy was taken as equivalent to that in mean-noon sunlight (Table II, column 3); this is the instance shown in Table I.

TABLE II. RELATIVE ENERGY DISTRIBUTION IN THE SPECTRUM

1 Spectral region	2 Range in A.	3 % relative energy in mean-noon sunlight (Abbot)*	4 % relative energy in blue sky light (Walsh; Atkins & Poole)	5 % relative energy in daylight (sun 2 + sky 1)†
Violet-blue	3800–4900	26·7	50	34·5
Green	4900–5600	24·2	24·3	24·2
Yellow	5600–6200	19·7	12·3	17·2
Red	6200–7200	29·4	13·4	24·1
		100	100	100

* Taken as the % relative energy in light from sun and cloud with no blue sky on August 28 1933.

† Taken as the % relative energy in mixed daylight during all other exposures in 1933 and 1934.

The total energy in air is derived from the illumination integral by taking the energy, within the visible spectrum, as 1·5 joules or 0·36 g.-cal. in 1 kl.-hr. per cm.²,* when the source of light is mean-noon sunlight.

The same conversion figure was also used for daylight, although only a portion of the energy comes from sunlight and the rest from the sky. This is possible, if a Burt sodium cell is used to measure the illumination integral, the constants for sunlight and sunlight with sky light being not very different for this type of cell, so that they may be taken as equal without serious error.

---

* *Conversion of kilolux-hours to joules.* The flux of light in .1 kl. (1000 metre-candles) on 1 cm.² is 0·1 lumen. If it be assumed that the luminous efficiency of daylight (3800–7200 A.) be 240 lumens per W. (= 1 joule or 10^7 ergs per sec.), the energy flux in 0·1 lumen is 0·1/240 or 0·00417 joules per sec. If the flux be maintained for 1 hr. (1 kl.-hr. per cm.²), the amount of energy transmitted will be 0·00417 × 3600, or 1·5 joules, or 0·36 g.-cal., taking the standard value of 4·183 joules as equal to 1 (15° C.) g.-cal. Poole & Atkins (1936, p. 377), give 269 lumens per W. as the luminous efficiency of mean-noon sunlight (4000–7600 A.). This has been modified to 240 lumens per W., for the present range of 3800–7200 A., on Poole & Atkins' suggestion, in view of the lower value of 223 lumens per W. found by them for Abbot's mean-noon sunlight (4000–7600 A.) by calculation.

To sum up, if we know the extinction coefficients for four adjacent spectral regions in sea water, the relative energy distribution between the four regions in air and the total energy represented by the illumination integral in air, it is possible to calculate the total radiant energy in the visible spectrum at any depth in the sea, during a given time. This is here called the energy integral, and expressed either in joules or gram-calories per square centimetre (Table I).

One other correction has been introduced, and that is the subtraction of a rather arbitrary amount from the illumination for the loss of light by reflexion from the surface of the sea (Table III, p. 308).

In Fig. 1, the "weighted energy percentages" for August 4 are plotted on a logarithmic scale against the depth on a plain scale; the figure shows that the colour of the illumination changes progressively with depth below the surface of the sea, since the slope of the straight line for each colour is determined by its extinction coefficient, and is different in each case. The particular case illustrated is typical of clear water in the English Channel, where red light is the most rapidly extinguished, green has the greatest penetrating power, blue follows closely on green, and yellow is intermediate between blue and red. The figure also shows the relative distribution of energy between the four spectral regions, blue, for instance, having the greatest share in air, but gradually losing its preponderance over green with increasing depth under water.

Although this change in colour of light at different depths in the sea is striking, its possible effect upon photosynthesis is outside the scope of the present work, in which the energy integral is assessed irrespective of the wave-lengths and the spectrum has only been subdivided for the purposes of making the assessment.

APPARATUS AND METHODS FOR MEASURING ILLUMINATION

Standards

All the photo-electric cells used for the present work were standardized for the measurement of visible light as described by Poole & Atkins (1935, p. 1). The calibration is in metre-candles, against a carbon arc (1935, p. 11) and "artificial mean-noon sunlight" (1935, p. 16). The two scales agree well in bright mixed daylight.

Illumination Integral

The vertical illumination integral (p. 304) is measured by means of a Burt sodium cell, mounted with its opal plate set horizontally on the roof of the Plymouth Laboratory (Atkins & Poole, 1930, p. 305; 1931*b*, p. 617).

This cell, when used in daylight, has its maximum sensitivity in the violet

TABLE III. DETAILS OF EXPERIMENTAL EXPOSURES, AND DATA USED IN CALCULATING SUBMARINE ENERGY

Station …	Eddystone Lighthouse, depth 60 m.					S. of Stoke Point, Shagstone bearing N. by W. depth 53 m.
	Bearing S.E.	Bearing N.W.	Bearing N.W.	Bearing S.E.	Bearing S.E.	
Date … Time of start, G.M.T.	July 25 1933 0945	Aug. 4 1933 0910	Aug. 28 1933 1140	July 12–13 1934 2120	July 19–20 1934 2035	Aug. 9–10 1934 *A*, 0630 *B*, 1032 *C*, 1434 *D*, 1835
Duration in hours …	6·25	5·58	5·17	23·7	22·7	*A*, 4 *B*, 4 *C*, 4 *D*, 11·5 = 23·5
Sea	Flat calm	Calm, with slight ripple	Moderate swell, rising	Fairly calm, rising to swell on 13th	Slight swell, rising considerably on 20th	Moderate, rising during 9th to heavy swell on 10th
Wind	None	Light E.	Light	Light S.W.	Fresh S.E., rising	Light N.W., veering to S.W. and rising
Sky	Overcast, clear after 1300	Clear, with brilliant sun	Overcast throughout	Sun and cloud, some rain on 13th	Sun to overcast	Sun, soon overcast
Illumination integral in kl.-hr.*	338	197	171	408	401	*A*, 108 *B*, 152 *C*, 93 *D*, 6·7
Secchi disk, average	12 m.	14 m.	13 m.	—	14 m.	11·5 m.
Extinction coefficients for:						
"Blue"	0·14†	0·12†	0·14	0·082	0·082	0·142
"Green"	0·13†	0·115†	0·13†	0·095	0·095	0·105
"Yellow"	0·16†	0·14†	0·16†	0·093	0·093	0·13
"Red"	0·48†	0·414†	0·46†	1–5 m. = 0·358 5–10 m. = 0·250 10–30 m. = 0·203	0·358 0·250 0·203	1–5 m. = 0·456 5–35 m. = 0·281

* Corrected for surface loss (p. 310).

† Derived from Secchi disk readings (p. 309).

region of the spectrum: nevertheless, it gives a "tolerably correct measure of the daylight" (Atkins & Poole, 1936*a*, p. 253, fig. 2). Thus, on a fine summer day, the recorded variations in intensity of violet light can be taken as indicative of the variations in intensity of daylight as a whole, at least between the hours of 0500 and 1900 G.M.T., when the colour of the daylight does not alter materially. All the short exposures fell between these hours; the 24 hr. exposures naturally included the hours before 0500 and after 1900, when the colour of daylight does alter quite appreciably, but during these hours the intensity is so low that the error introduced by estimating the total light from a measure of the violet light is scarcely significant.

It has been assumed that the illumination integral, measured on the roof of the Laboratory on the shore of Plymouth Sound, may be taken as a fair integration of the illumination during the same period at the surface of the sea about 10 miles to the south at the stations where the experiments were carried out. Uneven distribution of cloud over land and sea may sometimes have invalidated this assumption to some, but probably not to any very great, extent (p. 311).

*Extinction Coefficients**

The coefficients (p. 305) were not always determined in the same way. In 1933 Dr Atkins was prevented by illness from carrying out the full programme of photo-electric measurements; the extinction coefficient for blue light had therefore to be estimated from Secchi disk readings, on July 25 and August 4, but on August 28 Dr Atkins determined it directly with a gas-filled potassium photo-electric cell (Poole & Atkins, 1928, fig. 2, p. 466). The coefficients for green, yellow, and red for each of these days were derived from those for blue, by reference to the complete data obtained for four regions at the same station in the previous year (Atkins & Poole, 1933, table IV, pp. 150 *et seq.*).

In 1934 the extinction coefficients were measured by means of the Bergmann selenium rectifier cell (Poole & Atkins, 1933, pp. 538 *et seq.* and 1934, pp. 727–36), after correcting for the curvature of the relation between the current and illumination. On July 12 the coefficients for blue, green, and red were measured directly, leaving only yellow to be derived from the "yellow/blue ratio". On July 19 the Secchi disk reading showed a degree of transparency similar to that of the previous week, and the same coefficients have therefore been used for both days. On August 9, all four extinction coefficients were determined photo-electrically (Table III).

The Secchi disk readings, used for estimating the coefficients when no photo-electric measurements were available, were taken from the deck of S.S. *Salpa* and were strictly comparable with those taken in previous years (Poole & Atkins, 1929, p. 309), during the establishment of the empirical formula

$$\mu_{v_{0-20}} = 1{\cdot}7/D,$$

---

* Pettersson (1934, p. 7); "absorption coefficient" of Poole & Atkins' earlier papers; and "vertical transmissive exponent" of Clarke (1933, p. 317).

where μ_v is the vertical extinction coefficient for blue light, and D the maximum depth of visibility of the Secchi disk. Such a formula can only give a rough approximation, with no evidence as to the opacity of different water layers; but several series of measurements, made in the open water of the English Channel in the summer of previous years, seemed to show that there is very little change in opacity from depth to depth, and even from day to day, in the absence of heavy gales. Since the weather in July 1933 was exceptionally fine the coefficients derived from the Secchi disk readings may be taken as reasonably reliable.

Surface Loss

Atkins & Poole (1933, p. 148) give the loss of light by reflexion from the surface of the sea as varying between 2%, when measured during a glassy calm, through 5–17% for light winds, up to 25% for moderate winds; beyond this it is not practicable to determine the loss directly.

No direct measurements of the surface loss were made during any of the present exposures, but an arbitrary loss of 15% has been assumed for all the exposures, except the last, in spite of certain differences in the conditions at the sea surface (Table III).

For the last series of exposures on August 9–10 1934, the energy values have been plotted in Fig. 6 as though there had been no surface loss. This brought the curves for periods *A* (0630–1028 G.M.T.), and *B* (1032–1430) into the same relation with the points for oxygen production as in the previous year (Figs. 3–5); but left a discrepancy in the case of period *C* (1434–1828). By subtracting a surface loss of 33% from the value for *C*, the curve $C \times 0{\cdot}66$ (Fig. 6) was obtained and agreed more nearly with the oxygen-production points for the same period. So low a value for *C* was independently suggested by the evidence of a photographic light-recording apparatus exposed at sea during the experiment. This apparatus (constructed by Dr L. E. Bayliss) floated alongside the surface cage of bottles, with its window just awash, and gave a series of values for the illumination integrals, in which *C* was about 30% lower than the value obtained by the photo-electric recorder on the roof of the Laboratory at Plymouth. If these photographically determined values (kindly supplied to me by Dr Bayliss from unpublished data) are given in relation to an illumination integral of 108 kl.-hr. for period *A*, so as to be directly comparable with the photo-electrically determined values, we get the following figures:

August 9–10	Period *A*	*B*	*C*	*D*	
Kilolux-hours	93	130	52	5·5	Photographically determined at sea (Bayliss)
	108	151	60	6·4	The same, adjusted to 108 for period *A*
	108	152	93	6·7	Photo-electrically determined on shore

Considering the close concordance for periods *B* and *D*, after adjustment of *A*, the difference in the values for *C* is definitely significant. It may have been due to an uneven distribution of cloud reducing the light more at sea than at the laboratory; or it may have been due to the sea's being rougher during period *C* than earlier in the day (Table III) and causing greater reflexion loss at the surface, or to a combination of these factors.

With regard to surface loss, during periods *A* and *B*, it is suggestive that the subsurface illumination integral determined photographically at sea is just about 15%* lower than that determined photo-electrically in air (93–108). This agrees with the usual 15% allowed for surface loss during all the other exposures. The fact, therefore, that the energy values appear to fit the oxygen values for periods *A*, *B*, and *D*, without allowing for this loss, probably means that the diatoms were producing more oxygen per million cells for a given amount of energy than those of the previous year. This would have been quite possible if the cells had been larger or more active in 1934 but cannot be proved, as neither the size nor the activity of the cells was measured.

MATERIAL AND METHODS FOR MEASURING PHOTOSYNTHESIS

Choice of Diatoms

Biddulphia regia M. Schultze and *Coscinodiscus excentricus* Ehr. were both used for preliminary experiments, but the cells of the former were found to be too large and heavy to remain evenly distributed in the samples, or to give consistent results. *C. excentricus* was, therefore, used in all the experiments recorded below. It is an oceanic species of world-wide distribution; but in the English Channel it occurs most commonly in winter and early spring. The cells are disk-shaped and very regular in size, large enough to be counted easily or picked out with a pipette under a low-power binocular microscope, and less liable to damage than more irregular or spiny forms. Dr Lebour (1929, p. 36) gives the diameter of the cells as 50–90 μ, but it was noticed that the cells, in culture, decreased to about 40 μ as the summer progressed. They formed chains of two, four, six, or even eight loosely associated cells when the cultures were healthy, but these could be easily broken up by shaking in order to distribute the individual cells evenly in the samples.

Growth of Cultures

All the cultures were started from single cells from the early spring plankton, and were maintained in the laboratory for the following 6 months by making subcultures every 10–15 days. The cultures were grown in Allen & Nelson's (1910, pp. 427–8) "Miquel Sea Water" made up in "Berkefeld" filtered (*ibid.* pp. 432–3) "Outside Water", from the English Channel, with the addition of 1 ml. per l. normal $NaHCO_3$ and 3 mg. per l. SiO_2 (in the form of sodium silicate). Allen & Nelson (1910, p. 445) had shown silicates to be of value in increasing the uniformity of the cells of *C. excentricus*; and, although the amount of added silicate was not great,* control cultures showed that it was sufficient to improve the growth.

---

* When the photographic and photo-electric instruments were exposed side by side on the Laboratory roof they agreed to within 5%, giving respectively 505 and 480 kl.-hr. for the illumination integral on July 12–13 1934. The agreement may not be so close under water, but the 15% difference shown on August 9 is probably of the right order.

To reduce the bacterial content of the medium it was brought just to the boil (not to 70° C.) after addition of the nutrient salts; this precipitated much of the silicate with the ferric phosphate, leaving nitrates rather in excess. Dr L. H. N. Cooper, who kindly made some special analyses for me, found that the freshly prepared and boiled Miquel Sea Water contained about 2·5 mg. per l. P_2O_5 in solution, or about one-quarter of the amount added, and about 0·007 mg. per l. Fe. Culture medium, in which growth of diatoms had nearly come to a standstill, contained 2·25 mg. per l. P_2O_5, and at most 0·002 mg. per l. Fe (see Appendix, p. 343).

If this medium was kept in a covered vessel, and not inoculated, it remained quite clear for several months.

All the glass vessels used for cultures and experiments were sterilized by dry heat.

The stock subcultures were kept in 125 ml. flasks, containing 50–60 ml. of the medium, and closed by an inverted glass dish; the large quantities of culture required for the photosynthesis experiments were grown in 3 l. flasks placed in the north windows of the aquarium and screened by butter muslin to reduce the light intensity; four or five of these large flasks, if fairly heavily seeded, produced a sufficiently thick crop of actively growing diatoms for an experiment in about a week or 10 days.

The temperature in the aquarium ranged from about 15 to 19° C., with a short period in August 1933 when it rose to a maximum of 21° C. and stopped the growth of the cultures.

Sterility of the Cultures

Sterility from bacteria is difficult to attain in diatom cultures and cannot be claimed here with certainty, since no bacterial counts were made. It is also arguable that, although Dr Allen's unpublished plating experiments with similar cultures gave negative results, bacteria, which would not grow on agar, may yet have been present in the sea-water medium. On the other hand, the diatom cultures were apparently highly sensitive to bacterial infection and could only be grown freely after repeated washing in sterile culture fluid and treatment with iodine.* The resultant cultures showed none of the clouding characteristic of heavy bacterial infections, but remained crystal clear when left for 5 weeks or more.

---

* Atkins (1923, p. 156) showed that sea water, after boiling for 3 hr. in glass, may contain as much as 5·5 mg. per l. SiO_2. The heating, in the present case, is insufficient to have this effect.

It was therefore assumed that the cultures were at least free from serious bacterial infection.

Exposure of the Diatoms in the Sea

After a number of preliminary experiments, photosynthesis in the sea was estimated by the following elaboration of Marshall & Orr's method (1928, fig. 1, pp. 321 *et seq.*).

Six bottles were exposed at each depth chosen for investigation: three round 180 ml., clear-glass, reagent bottles (*R*, Fig. 2) exposed to light from all sides; two slightly smaller, rectangular, medicine bottles (*F*) blackened on all sides but one, which faced upwards to receive only light falling on a horizontal surface; and one round bottle (*B*) enclosed in a double black-cloth bag and thereby protected from all light. The "flat" medicine bottles were included for comparison with the photo-electric cells which are also affected only by light falling on a horizontal surface.

All the bottles were sterilized and filled from a uniform mixture of about 15 l. of diatom culture and an equal volume of fresh Miquel medium. Cultures of the same age and strain were always selected for any one experiment. In 1933 the culture was mixed by hand in two sterilized earthenware jars; in 1934 it was mixed and aerated for 3 hr. by compressed air led in through a distilled water trap and a cotton-wool plug. The bottles were filled with the mixture, by means of a glass siphon, in a dim light;† they were then kept in the dark until they were lowered into the sea, except for a short exposure to dim light while being tied into galvanized iron wire cages (Fig. 2) in the ship's cabin.

At the beginning of all experiments, and also at the end of long experiments, 2 or 5 ml. samples of the culture were fixed with formalin so that the diatoms might be counted at leisure.

The wire cages were each slung by cords from all four corners, so as to hang horizontally. They were attached to a buoyed cable, 155 m. long and weighing 22 kg., anchored in 55–65 m. of water. Cages below 5 m. from the surface were hooked to the cable by halyard swivels; the surface cage floated in a wooden frame that cast no shadow on the bottles and was tied to the end of a 3 m. floating, bamboo pole, tied in turn to the buoy; cages between the surface and 5 m. were slung from the pole to avoid the shadow of the buoy.

---

* The cells were placed for a minute or two in 2 drops of 0·006 N iodine in 50 ml. Miquel Sea Water and then returned to pure Miquel. This treatment was suggested by Dr Allen as a result of experiments on the effect of chlorine and iodine on his cultures. Miss D. M. Mees recommended repetition of treatment in 3 days, instead of at the time of the next routine subculture, to prevent spore formation; this led to further improvement in the growth of treated cultures.

† 210 V. lamp run at 100 V. in a dark cellar.

A 14·5 kg. weight was attached to the cable just below the lowest cage, so that the part of the cable with the bottles attached to it should hang as nearly vertical as possible. As the cable was anchored, strong tides and wind would displace it to a greater or lesser degree from the vertical. No correction has been applied for the unknown extent of this deviation.

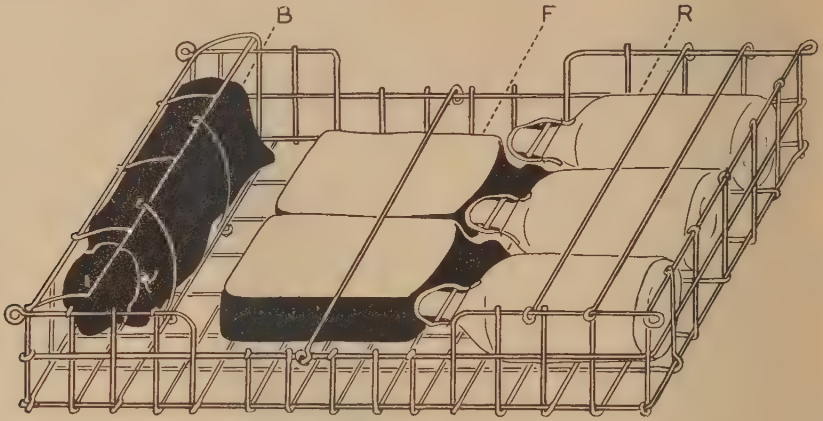


Fig. 2. Cage and bottles in which the diatoms were exposed in the sea (isometric projection). *R*, the three round, clear-glass bottles, exposed to full light; their stoppers are secured by strips of rubber tied over them. *F*, the two flat medicine bottles, blackened on all sides save the uppermost horizontal surface; the contents of these bottles received the same illumination as a photo-electric cell, and were partially shaded, as compared with *R*. *B*, the bottle protected from all light by a black bag of double cloth; this served to measure respiration only.

Lowering or raising the cages took about 2 min., during which time the bottles belonging to the lower levels in the experiment were exposed to considerably greater illumination than at their intended positions. In the 24 hr. experiments in 1934 this error was eliminated by lowering and raising the cages after dusk.

The buoy was anchored at one of two stations in the clear, open, water of the English Channel (Table III), where the transparency of the water did not vary appreciably with the change of the tide, as it might have done nearer the shore. This choice of station made it necessary to choose relatively calm days for the experiments: on rougher days the wind and Atlantic swell coming up the Channel would have made it impossible to shoot or lift the gear safely because of the rolling of the ship. Even the drift due to neap tides, if increased at all by wind, made it extremely difficult to lift. The calmer days in 1933 were also days of almost unbroken sunshine, giving steady illumination that could be accurately measured; in 1934 the calmer days were usually overcast.

TABLE IV. PHOTOSYNTHESIS EXPERIMENT, JULY 25 1933. 0945–1605 G.M.T. EXPOSURE OF DIATOMS IN "ROUND" BOTTLES ONLY

Initial oxygen content = 4·872, 4·829, 4·801 ml. per litre.
Culture of *Coscinodiscus excentricus* containing 296 cells per ml.

	Oxygen in ml. per litre			Oxygen in ml. per 10^6 cells
Depth in metres	Light (*l*)	Dark (*d*)	Increase (*l–d*)	Total (*l–d*)
0	5·547	4·829	0·703	2·38
	5·530		0·686	2·32
	5·482		0·638	2·16
1	5·569	4·812	0·725	2·45
	5·514		0·670	2·26
	5·564		0·720	2·43
2	5·849	4·829	1·005	3·40
	5·706		0·862	2·91
	5·760		0·916	3·10
4	6·271	4·845	1·427	4·82
	6·239		1·395	4·71
	6·244		1·400	4·73
6	6·123	4·878	1·279	4·32
	6·238		1·394	4·71
	6·310		1·466	4·95
8	6·178	4·873	1·334	4·51
	6·190		1·346	4·55
	6·200	Av. 4·844	1·356	4·58
10	6·348	5·026	1·293	4·37
	6·376		1·321	4·46
	6·370		1·315	4·44
15	5·981	5·048	0·926	3·13
	5·926		0·871	2·94
	5·997		0·942	3·18
20	5·531	5·043	0·476	1·61
	5·613		0·558	1·89
	5·547		0·492	1·66
30	5·130	5·081	0·075	0·25
	5·213		0·158	0·53
	5·141		0·086	0·29
40	5·054	5·075	0·000	0·00
	5·092		0·037	0·13
	5·059	Av. 5·055	0·004	0·14

Estimation of Oxygen

At the beginning of the exposure in the sea Winkler reagents* were added to at least three "initial" samples of culture; at the end, the reagents were added to all the bottles that had been in the sea, the six in each cage being treated in quick succession with as little further exposure to light as possible. Each bottle was then carefully shaken and sealed with water held in a rubber sleeve surrounding the stopper.

Weather permitting, these reagents were added on board ship, but in any case with the least possible delay, the bottles being kept in the dark in the interval; it was then assumed that any additional oxygen consumption, which might have occurred in that interval, would be the same in the bottles in dark bags and in those which had just been removed from light in the sea, and would therefore cancel out in calculating the total oxygen production in the light. It was found, however, that the respiration of the cultures was barely measurable even after 2 hr. in the dark.

After allowing the precipitate to settle for 1 hr. in the Laboratory, hydrochloric acid was added to the samples, which were then stored under water until required for titration.

In 1934 only 100 ml. from each bottle was titrated in a slow stream of nitrogen; these samples were taken in a random order, to avoid prejudicing the results by knowing the bottle's position in the experiment. In 1933 the bottle's position was known, but the volume of the sample was varied by titrating the entire contents of each bottle.

* 45 % $MnSO_4, H_2O$ (40 % $MnCl_2, 4H_2O$ on July 25 1933); 15 g. NaOH and 5 g. KI in 100 ml. H_2O; *N*/100 KIO_3 as standard; *N*/200 $Na_2S_2O_3, 5H_2O$ for titration; and 1 % starch solution preserved in 20 % NaCl as indicator.

Calculating and Recording the Results

The oxygen in each bottle was first calculated in ml. per litre at N.T.P., as recorded in Tables IV–VII (pp. 315, 320, 325, 329). These figures were then converted into ml. of oxygen per million diatom cells, so that the results of experiments with different concentrations of diatoms might be compared directly (Table IV).

Then, in order to bring the results into line with those of Marshall & Orr (1928, p. 324) and others, the "total oxygen production" was calculated and recorded in the graphs (Figs. 3–8). "Total oxygen" is obtained by adding to the "net" amount of oxygen produced in the light an amount of oxygen equal to the average amount consumed by respiration in the dark. This calculation is based on the commonly accepted view that plants respire continuously at a constant rate, whether they be kept in the dark or exposed to light. In theory, at least, this assumption may well be queried (Montfort & Neydel, 1928, p. 810); but it is not easy to test in practice, owing to the apparent impossibility of separating the gaseous exchange due to photosynthesis from that due to respiration. As the future may elucidate this problem and show the present assumption to be invalid, the original observations, rather than the derived values plotted in the figures, are recorded for reference in Tables IV–VII.

The amount of oxygen added for respiration, in the present case, is small, and the procedure has the advantage of eliminating negative values for samples exposed to such weak light that oxygen production does not exceed consumption.

There were some minor differences in the treatment of data from the first and last experiments, compared with the rest, to allow for different experimental conditions. For July 25 1933, the total oxygen was taken directly as the difference (*L–D*) between the oxygen in bottles after exposure to light (*L*) and dark (*D*) as in Table IV.

For experiments from August 4 1933 to July 19 1934 a more exact method was used, allowing for differences in the initial values (*In*) of different portions of the large quantities of culture. The net oxygen production (*L–In*) was calculated for each bottle in ml. per million cells; the respiration value (*In–D*) was calculated for the sample at each depth, and then averaged for groups of bottles exposed to roughly similar temperatures (e.g. 0–10 and 12·5–40 m., Tables VI–VII). The total oxygen production, (*L–In*)+(*In–D*), was then plotted in Figs. 3–8 against the depth; each bottle exposed to the light being recorded separately to show the degree of divergence due to experimental error.

For the short exposures the results are all plotted on the same scale (Figs. 3–5); for the 24 hr. exposures the oxygen is plotted for convenience half-scale, relative to the depth (Fig. 8).

For August 9–10 1934, when the daytime exposures only lasted for 4 hr. each, the net oxygen production has been plotted (Fig. 6), as the respiration was not measured. Measurements of respiration on the same culture during the night, showed that it amounted to about 0·09 ml. per million cells in 4 hr., and would therefore have been almost within the general experimental error.

The sea temperatures during the exposures are plotted on the appropriate graphs.

Accuracy of Methods used in Estimating Photosynthesis

The standardization of thiosulphate for titration was accurate on the average to ±0·14%, or about 0·008 ml. per l. O_2. All calculation of oxygen values was therefore carried to three places of decimals (Table IV), and the results recorded after correction to two places. Complete Winkler estimations, carried out upon sets of identical samples in the laboratory, were then found to agree to within ±0·2%, or 0·01 ml. per l. O_2. Similar estimations on triplicate samples of diatom culture, after supposedly identical exposure to light in the sea, agreed, on the average, to within about ±1% in 1933 (0·06 ml. per l. with maximum difference in one case of 0·4 ml. per l.), and less in 1934 (0·05 ml. per l., with maximum in one case of 0·19 ml. per l.). The error here includes discrepancies due to mixing (improved in 1934) and sampling of the diatom culture, any lack of uniformity in behaviour of the diatoms themselves, or in their exposure to light, as well as the inevitable loss of accuracy in the Winkler estimation due to the motion of the ship while the reagents were being added to the bottles.

Respiration values at similar temperatures differed by 0·11 ml. per l. in 1933, and 0·04 ml. per l. in 1934, in any one experiment; for this reason the values have been averaged. Respiration for different cultures varied from 0·02 to 0·12 ml. oxygen consumed per million cells per hour. This large variation may have been due in part to difference in size of the cells, but must also indicate a difference in activity of different cultures, and possibly (as suggested to me by Dr S. A. Waksman) some difference in bacterial infection.

The error in counting the diatoms was well within 1%; the error in sampling was nearly 5%, if 2 ml. samples containing about 600 cells were taken. The absolute error in such a sampling method is of the order of $\sqrt{n}$, where n is the number of the cells in the sample; the error in the present case was, therefore, at least halved by increasing the size of the sample to 5 ml.

The size of the diatom cells varied appreciably in different strains, and that of the same strain decreased as the summer advanced. No allowance has been made for these differences, except in the analyses recorded in the appendix (p. 343) and referred to in the discussion (p. 338). No estimates of dry weight of the diatoms were made.

FACTORS INFLUENCING THE RATE OF PHOTOSYNTHESIS DURING THE EXPOSURES AT SEA

Although no photosynthesis can occur in the absence of energy in the form of light, it is well known (e.g. Spoehr, 1926, p. 95) that the rate at which it proceeds, even in the presence of light, may be profoundly influenced by a number of other factors, any one of which may act as the "limiting factor" (Blackman, 1905, p. 281) by being present in either an inadequate or excessive amount.

It is, therefore, clearly essential to examine the possible influence of such factors in the present experiments, before considering the effect of energy upon the rate of photosynthesis.

The external factors to be examined are:

(1) The supply of nutrient salts.
(2) The osmotic pressure of the medium.
(3) The hydrogen-ion concentration of the medium (*p*H).
(4) The partial pressure of the carbon dioxide (CO_2) in the medium.
(5) The temperature.

The internal factors are:

(6) The amount and composition of the chlorophyll, and other pigments in the cells.
(7) Certain protoplasmic, or enzymatic factors.
(8) The accumulation of end-products of photosynthesis either within the cells or in the medium.

Limitations due to anatomical structure and to the translocation of end-products do not arise in the present case, since the plants used were unicellular.

External factors

The Miquel Sea Water medium, in which the diatoms were grown, has been shown to supply them with ample nutrient salts for long-continued growth, as well as a suitable osmotic pressure and *p*H. All the experiments were carried out in this medium.

The medium apparently supplies an excess of CO_2, for the additional sodium bicarbonate raises the excess base to $2{\cdot}7/1000\,N$, the total CO_2* to about 56 ml. per l., and the free CO_2 to about 0·75 ml. per l. when the medium is freshly made up at about *p*H 7·8. After aeration some CO_2 may be lost, raising the *p*H to 8·1 or 8·2: but, even then, laboratory experiments showed that this medium could yield about 2·75 ml. per l. CO_2† during a few hours, while in the experiments at sea the amount consumed was never more than 2·0 ml. per l. CO_2, with a rise of less than 0·18 *p*H. It is still possible that, in accordance with Harder's findings (1921, pp. 550 *et seq.*), CO_2 may have been affecting the rate of photosynthesis, for he showed that, even when neither CO_2 nor light was acting as a direct limiting factor, a richer supply of CO_2 would yet lead to higher oxygen production for a given light intensity. This is theoretically important in the present case, but it may be set aside in practice, since the supply of CO_2 in the experimental medium was already richer than would ever be available in the sea naturally; and, even if the values obtained do not show the absolute maximum for oxygen production in the given light intensities, the experiments are still directly comparable with one another.

---

* I am indebted to Dr L. H. N. Cooper for the data on CO_2, obtained by extrapolation from figures of Buch, Harvey, Wattenberg & Gripenberg (1932, p. 58).

† Assuming a 1 : 1 ratio between CO_2 consumed and O_2 produced.

The temperature of the diatoms during an experiment must have been the same as that of the sea in which they were suspended. They were, therefore, not all at the same temperature, for the English Channel in summer has a thermocline. The greatest difference in temperature, however, between one depth and another in any one experiment was 4·2° C. (see Figs. 4, 5). No correction has been made for temperature differences, as no certain data were available as to their effect. If other factors, including light, were favourable, and photosynthesis were being limited by the effect of temperature on the "dark (chemical) reaction", an increase in temperature of 4° between 15 m. and the surface might be expected to increase the rate of photosynthesis by about 40%. Figs. 3–7 show that the rate actually decreased towards the surface, and could not therefore have been directly controlled by temperature. On the other hand, the surface temperature may have been so high as to have been damaging the cells, but this appears improbable, since the maximum temperature in the sea was 17·2° C. and the cultures were grown successfully in the aquarium at temperatures up to 19° C. The harmlessness of the sea temperatures may also be deduced from the successive 4 hr. exposures *A–C* on August 9 1934, when there was no appreciable fall in the rate of photosynthesis towards the surface in the first and last periods, whereas there was a sharp fall in the intermediate midday period. There can hardly have been a significant difference in the temperature of the sea between midday and afternoon, to account for the difference in behaviour of the diatoms.

Internal factors

The only practicable method of controlling the chlorophyll content and other internal factors was always to use actively growing cultures of similar age and closely allied strain and to expose them to identical treatment prior to the experimental exposure.* This at least gave consistent results, whereas cultures of different ages, when compared under controlled light and temperature conditions in the Laboratory, did not give the same ratio between oxygen production per hour and chlorophyll content (as measured by Harvey's method, 1934, p. 770).

---

* Montfort & Neydel (1928, p. 824) have shown clearly the effect of the prior illumination on the rate of photosynthesis.

The accumulation of end-products of photosynthesis within the cell should lead to cell division and growth, and there is no reason to suppose that this normal process was interfered with in the experiments: but no data are known that would show how closely cell division keeps pace with photosynthesis in these diatoms, or how far their rate of photosynthesis may be retarded by increase of end-products towards the end of a long exposure. The diatoms were kept in the dark for some hours before each experimental exposure so as to eliminate previously accumulated products as far as possible. Therefore their re-accumulation only seems likely to have had an appreciable effect upon the rate of photosynthesis towards the end of the whole-day exposures.

TABLE V. PHOTOSYNTHESIS EXPERIMENTS, AUGUST 9–10 1934

Depth in metres	Period *A*	*B*	*C*	*D*
	Oxygen in ml. per litre, after exposure to light			
0	6·56	5·66	6·05	5·31
	6·58	5·72	6·03	5·31
	6·51	5·71	6·04	5·31
2·5	6·22	5·85	5·97	Lost
	6·31	5·83	5·99	
	6·30	5·89	5·93	
5·0	6·57	6·25	5·95	Lost
	6·62	6·12	5·99	
	6·58	6·18	6·00	
10	6·10	6·09	5·74	Lost
	6·26	6·06	5·77	
	6·20	6·04	5·73	
17·5	5·63	5·66	5·39	Lost
	5·60	5·55	5·40	
	5·61	5·59	5·40	
25	5·30	5·31	5·25	5·16
	5·27	5·32	5·25	5·17
	5·24	5·33	5·21	5·17
35	—	5·20	—	5·18
	—	5·22	—	5·17
	—	5·21	—	5·19

Depth in metres	Period *A*	*B*	*C*	*D*
	Oxygen in ml. per litre after exposure in dark			
0	—	—	—	5·14
25	—	—	—	5·17
35	—	—	—	5·18

Oxygen in ml. per litre in initial samples

A	*B*	*C*	*D*
4·98	5·13	5·17	5·22
4·98	5·18	5·09	5·24
4·96	5·12	5·20	5·25
—	5·02	—	5·31

Number of diatom cells per ml.

A	*B*	*C*	*D*
672	386	411	331

Sunrise at Plymouth 0456 G.M.T.

Sunset at Plymouth 1946 G.M.T.

The accumulation of oxygen, as an end-product, in the surrounding medium may have a retarding effect upon the rate of photosynthesis, for Spoehr (1926, p. 169) quotes results to show that the rate in air may be reduced to one-third by an increase in the partial pressure of oxygen from 0·02 to 1 atmosphere. Retardation would be very slight in the present experiments, since the greatest increase in the partial pressure of oxygen in the medium, during an exposure, was less than 0·1 atmosphere.

It therefore appears that the factors which may possibly have been limiting the rate of photosynthesis in the present case were shortage of CO_2, low temperatures in the deeper exposures, and accumulation of end-products.

Now the characteristic "limiting factor" of Blackman (1905, p. 289) would check the rate of photosynthesis at a steady maximum, despite the further increase in amount of other favourable factors. It is clear that in the results shown in Figs. 3–7 no such limiting factor is directly in control of the oxygen production, for after reaching a maximum there comes a point when further approach towards the surface, with increasing light intensity, does not even maintain a steady rate of oxygen production but results in a marked decrease.

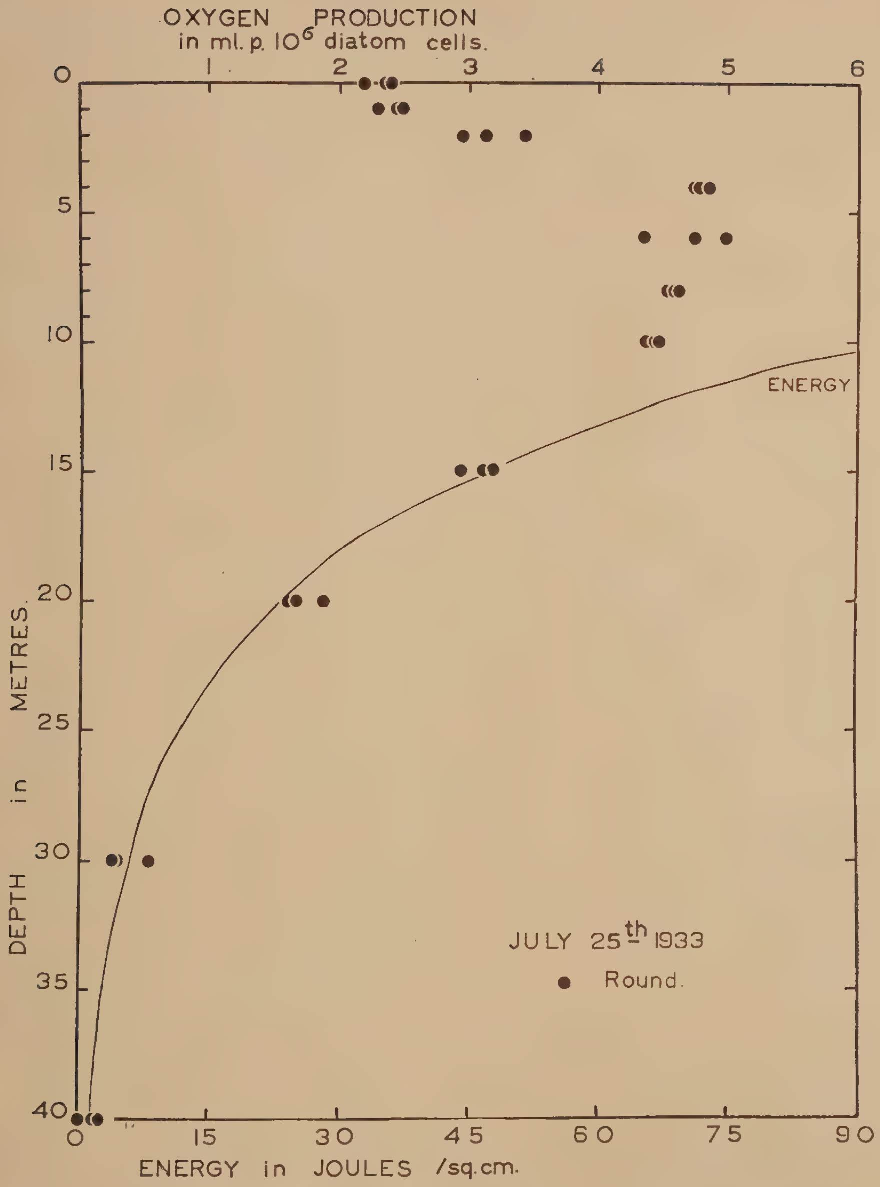


Fig. 3. Photosynthesis experiment with *Coscinodiscus excentricus* at L 5 on July 25 1933, using round bottles only. Each spot shows the total oxygen production (*l–d*) as measured in one of the three round bottles at any depth. The plain curve shows the total available energy (energy integral) during the exposure, as computed from measurements of the illumination integral and the extinction coefficients for blue, green, yellow, and red light. The exposure lasted from 0945 to 1605 G.M.T.

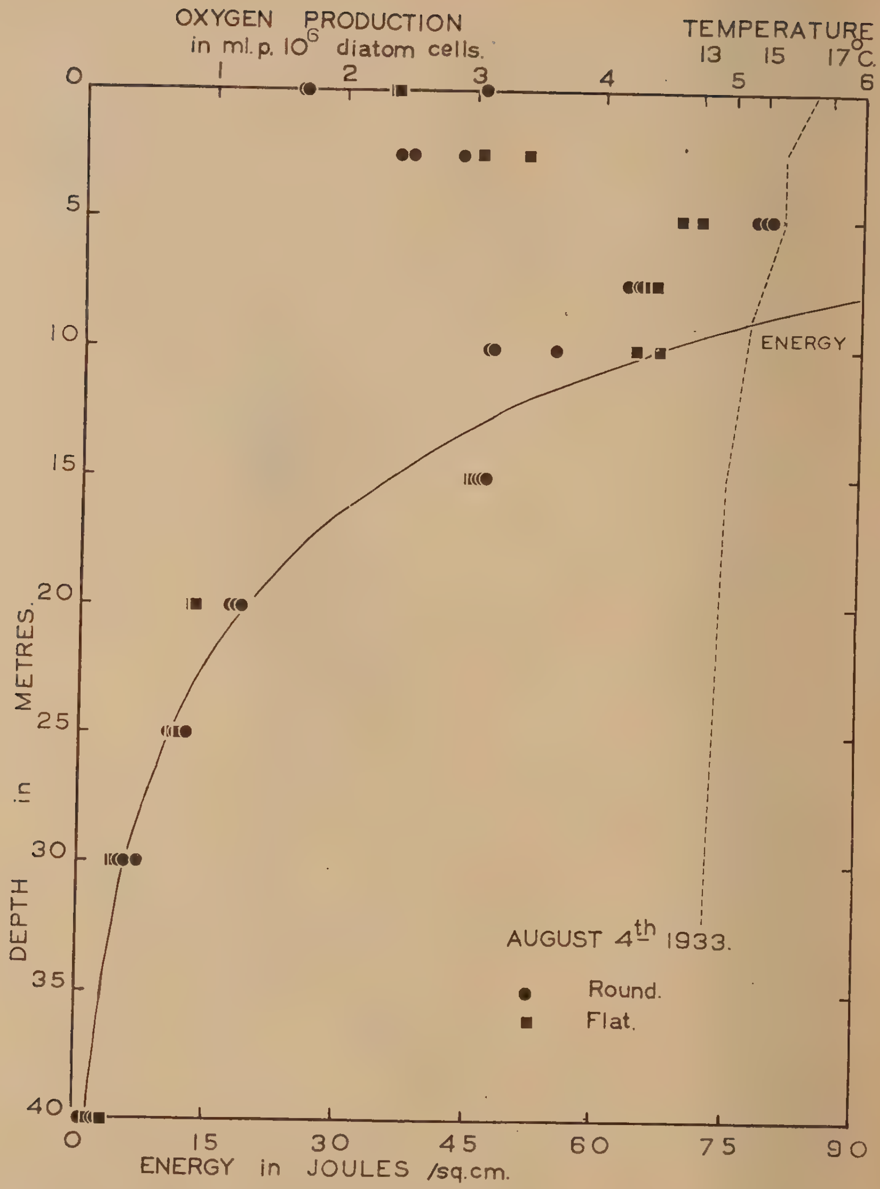


Fig. 4. Photosynthesis experiment with *Coscinodiscus* at L 5 on August 4 1933, shown on exactly the same scale as Fig. 3. The exposure lasted from 0910 to 1445 G.M.T. The round spots represent the total oxygen production (*l–In*) plus (*In–d*), in round bottles, and the squares that in flat bottles. The plain curve represents the total available energy, computed as for Fig. 3. The dotted curve represents the temperature of the sea during the experiment.

The measurements of both the photosynthesis and the energy in the sea may therefore be examined on the assumptions that the illumination is the only remaining variable upon which the rate of photosynthesis can be dependent, and that changes in the wave-length of the illumination do not affect the rate so long as the total energy in the illumination remains the same.

RESULTS OF THE EXPERIMENTS

On the first five occasions recorded here, the position chosen for the experiment was close to Station L 5 by the Eddystone Lighthouse; on the sixth and last occasion, August 9–10 1934, the position lay to the south of Stoke Point, 4 miles south by east of the Shagstone.

The experimental exposures may best be considered in four groups, according to the time of day at which they were made and their duration; there were three 5–7 hr. exposures round midday in July and August 1933; three successive 4 hr. exposures during daylight on August 9 1934; one night exposure of 11·5 hr. on August 9–10 1934; and two 24 hr. exposures in July 1934.

Three short Exposures in 1933 (Tables III, IV and VI, and Figs. 3–5)

The exposures were made on July 25 (Fig. 3), August 4 (Fig. 4) and August 28 (Fig. 5), and lasted between 5 and 7 hr. round midday. The weather was comparatively fine on each day (Table III), but was especially calm on July 25.

The plain curves in Figs. 3–5 represent the total energy integrals (p. 307) in joules, available during the exposure, plotted against the depth in metres. The amount of energy decreases almost exponentially with depth (Fig. 1).

The circles in Figs. 3–5 show the total oxygen production per million diatom cells in round bottles. Below a certain depth it can be seen that the oxygen values fall fairly closely on the curves for energy; this critical depth varies from 10 to 15 m. on the different days, but corresponds to an energy integral of about 7·5 joules or 1·8 g.-cal. per cm.^{2} per hr. on each occasion. Above this depth the oxygen values fall short of the energy curve, the divergence being greatest towards the surface, thereby suggesting an inhibitory effect due to the stronger light.

On August 4 and 28 flat, partially shaded, bottles (Fig. 2, *F*) were exposed, as well as the round bottles; the results are shown by the black squares, and are interesting in connexion with this possible inhibitory effect. At the lower levels the flat bottles give results that are not significantly different from those in the round bottles; but, in the upper layers where inhibition is suggested, there is a distinct tendency for the shaded bottles to give a higher value for oxygen production than the fully illuminated round bottles (Fig. 5), thereby supporting the hypothesis which attributes the inhibition to too much light, rather than to any effect of temperature.

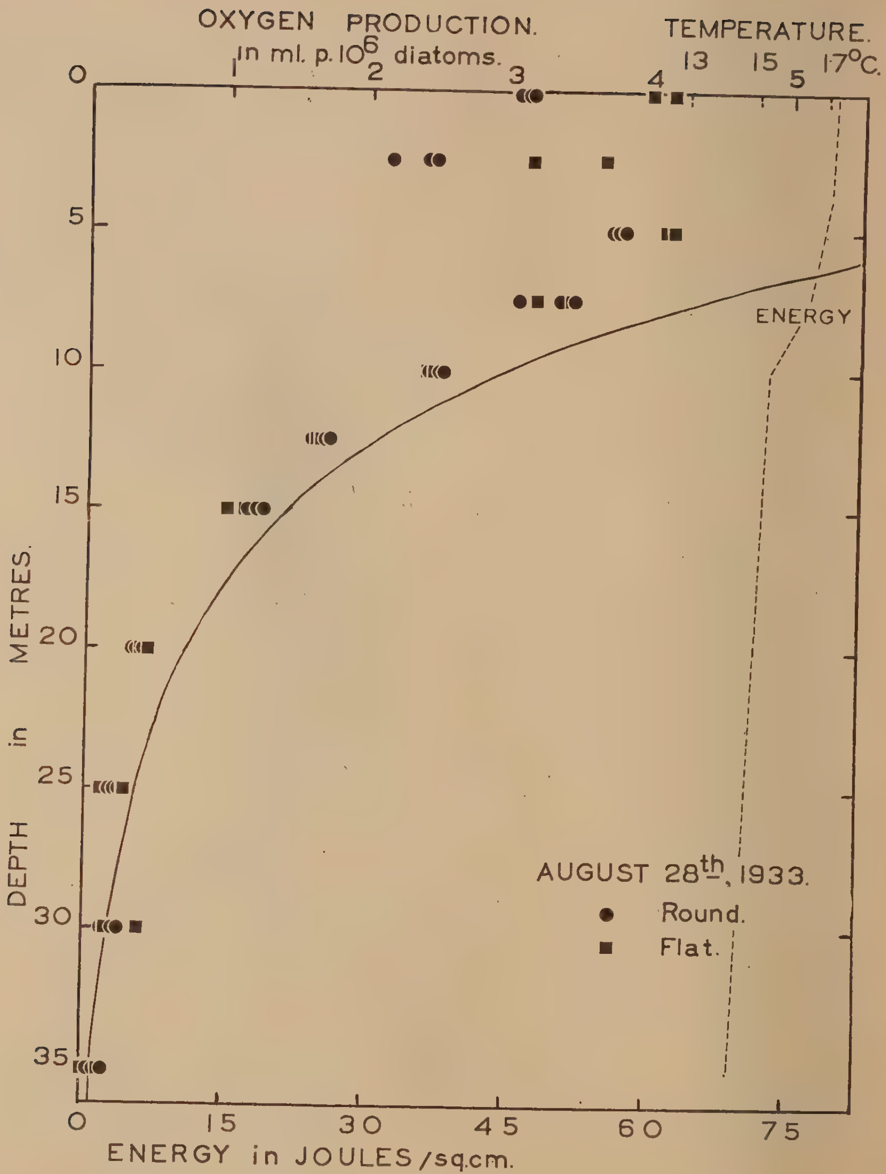


Fig. 5. Photosynthesis experiment with *Coscinodiscus* at L 5 on August 28 1933, shown on the same relative scales as Figs. 3 and 4. The exposure lasted from 1140 to 1650 G.M.T. Symbols and curves as in Fig. 4.

Successive four-hour Exposures in 1934 (Tables III and V and Figs. 6 and 7)

Three successive 4 hr. exposures were made on August 9 1934, starting at 0630 G.M.T. (Table III). The sky became increasingly overcast and the sea grew rougher as the day passed.

The plain curves in Fig. 6 again represent the energy integrals as computed from the photo-electric measurements made during the exposures.

TABLE VI. PHOTOSYNTHESIS EXPERIMENTS, AUGUST 1933. EXPOSURE OF DIATOMS IN ROUND BOTTLES (*R*) AND FLAT BOTTLES (*F*) (SEE FIG. 2)

		Oxygen in ml. per litre			
		Aug. 4 0910–1445 G.M.T.		Aug. 28 1140–1650 G.M.T.	
Depth in metres	Bottle	Light (*l*)	Dark (*d*)	Light (*l*)	Dark (*d*)
0	*R*	5·35 5·34 5·75	4·87	6·36 6·34 6·39	5·12
	F	5·56 5·57	—	6·48 6·42	—
2·5	*R*	5·57 5·60 5·70	4·80	6·10 5·99 6·01	5·14
	F	5·86 5·76	—	6·13 6·31	—
5	*R*	6·41 6·37 6·41	4·82	6·62 6·64 6·65	5·18
	F	6·21 6·25	—	6·47 6·48	—
7·5	*R*	6·09 6·12 6·12	4·84	6·47 6·51 6·35	5·13
	F	6·16 6·15	—	6·24 6·15	—
10	*R*	5·92 5·78 5·78	4·93 Av. 4·85	6·09 6·12 6·12	5·13
	F	6·17 6·11	—	5·91 5·89	—
12·5	*R*	—	—	5·81 5·81 5·76	5·03
	F	—	—	5·62 5·61	—
15	*R*	5·80 5·81 5·81	4·90	5·56 5·62 5·61	5·11
	F	5·76 5·76	—	5·44 5·39	—
20	*R*	5·26 5·26 5·24	4·92	5·27 5·24 5·24	5·03 Av. 5·11
	F	5·14 5·14	—	5·20 5·19	—
25	*R*	5·14 5·11 —	4·90	5·12 5·12 5·12	5·02
	F	5·08 5·09	—	5·15 5·09	—
30	*R*	5·00 5·04 5·00	4·89	5·13 5·12 5·10	5·06
	F	4·96 4·96	—	5·07 5·06	—
35	*R*	—	—	5·07 5·08 5·06	5·05 Av. 5·04
	F	—	—	5·05 5·02	
40	*R*	4·95 4·95 4·92	4·89	—	—
	F	4·95 4·92	—	—	—
50	*R*	4·90 4·94 4·92	4·91 Av. 4·90	—	—
	F	4·92 4·90	—	—	—
		Initial contents			
		O_2 (*In*)	Cells per ml.	O_2 (*In*)	Cells per ml.
0–20	*R*	4·87 4·90	293	5·25 5·26	405
25–50	*R*	4·90 4·93	293	5·18 5·19	405
0–50	*F*	4·87 4·92	293	5·20 5·15	345

Joules are plotted on the same scale, relative to depth, as in the previous graphs; but the energy integrals are slightly magnified by making no deduction for reflexion loss; a second curve ($C \times 0·66$, Fig. 6) for the third period shows the energy integrals after deducting 33 % for reflexion loss. This deduction is partly based upon photographic measurements of the subsurface illumination integral (p. 310).

The net (not "total", see p. 316) oxygen production is shown by squares for the morning period *A*, by circles for the midday period *B*, and triangles for the afternoon period *C*. For simplicity only the results obtained in round bottles are shown; but they were confirmed by flat bottles, as in the August experiments of the previous year. Below about 15 m. (Fig. 6) the oxygen values again fall fairly close to the energy curve for the corresponding period. Above 15 m. the oxygen values for the early morning and afternoon periods, *A* and *C*, increase slightly up to 5 m., though falling far behind the energy curve, and then remain practically constant to the surface, in spite of the rapid increase in energy: the oxygen values for the midday period, *B*, increase in the same way up to 5 m.; but, above this, they show a marked decrease towards the surface, just as in the experiments in the previous year, when the light at the surface was bright (Figs. 3–5). The coincidence of all values at 2·5 m. would seem to be fortuitous.

The oxygen values for period *C* fall closer to the curve $C \times 0{\cdot}66$, than to the curve $C \times 1$. Though a 33 % reflexion loss is rather high, it seems more accurate to assume some such change in the subsurface illumination (p. 310) than to postulate a change in the activity of the diatoms used in the third period, as compared with those used in the other periods, since diatoms of the same age and strain were used for all three periods. All the oxygen values are high during these exposures compared with the previous year (p. 311).

Night Exposure in 1934 (Tables III and V, and Fig. 6)

The night exposure (period D) followed immediately on the 4 hr. daytime exposures; it started at 1835 G.M.T. on August 9 and lasted 11·5 hr., that is until 0608 on August 10. The sea conditions were considerably rougher than during the preceding day and three of the cages of bottles were lost, so that no results were obtained from depths between the surface and 25 m. At 25 and 35 m. the oxygen content of the clear glass bottles was the same as that of the darkened bottles, showing that although the exposure started 2 hr. before sunset and lasted until 2 hr. after sunrise, the amount of energy penetrating to a depth of 25 m. or below, was insufficient to produce a detectable quantity of oxygen by photosynthesis. There was a slight production of oxygen at the surface during this period, agreeing fairly closely with the measure of available energy.

The results for these successive 4 hr. periods, and the night period, covering together 23·5 hr., are replotted in Fig. 7, with the oxygen as ordinates, and the time of day as abscissae, for the various depths. The relation of the oxygen production to the waxing and waning of daylight is clearly shown, as well as the midday inhibition near the surface; this result is closely similar to that obtained by Marshall & Orr (1928, fig. 7, p. 328) for a sunny summer day in the Clyde. The similarity is emphasized by the similar method of plotting, which allows the two sets of results to be compared directly.

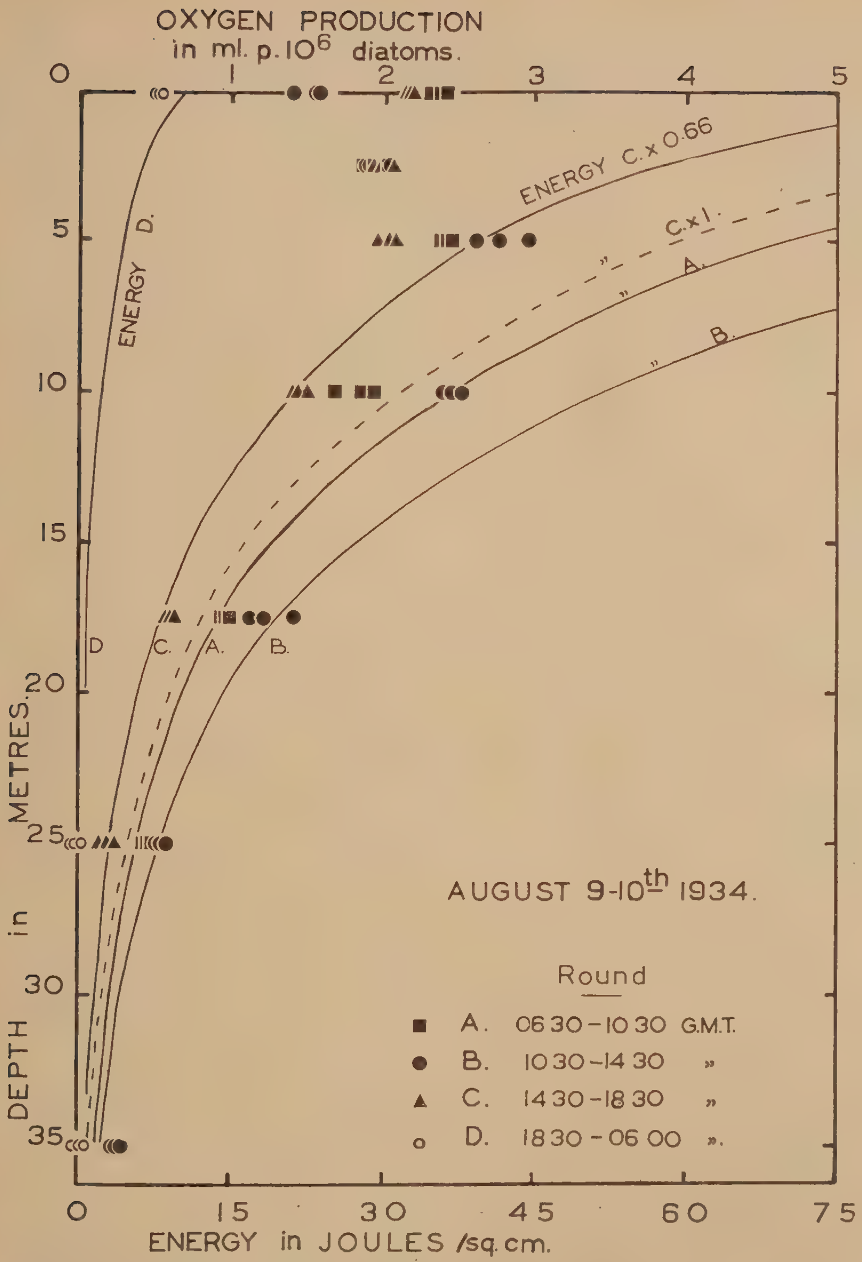


Fig. 6. Photosynthesis experiments with *Coscinodiscus* off Stoke Point on August 9–10 1934, shown on the same relative scales as Figs. 3–5. The exposures were made in three successive 4 hr. periods, *A*–*C*, during the day, and an 11·5 hr. period covering the night; period *A* lasted from 0630 to 1028 G.M.T., period *B* from 1032 to 1430, period *C* from 1434 to 1828, and period *D* from 1835 to 0608. The net oxygen production (*l*–*In*) is shown, for round bottles only, by squares for period *A*, rounds for *B*, triangles for *C*, and rings for *D*. The total available energy is shown without subtraction of surface loss (p. 310) for periods *A*, *B* and *C* (curves *A*, *B* and *C* × 1), and after subtracting 33 % surface loss for period *C* (curve *C* × 0·66). The temperature of the sea, on the morning of August 9, was 14·75° C. at 5 m., 14·40° C. at 15 m., 13·78° C. at 25 m., and 13·57° C. at 45 m.

Twenty-four-hour Exposures in 1934 (Tables III and VII and Fig. 8)

The first of these exposures began at 2120 G.M.T. on July 12 and lasted 23 hr. 40 min.; the second began at 2035 on July 19 and lasted 22 hr. 40 min. Both were slightly curtailed by the onset of rough weather (Table III).

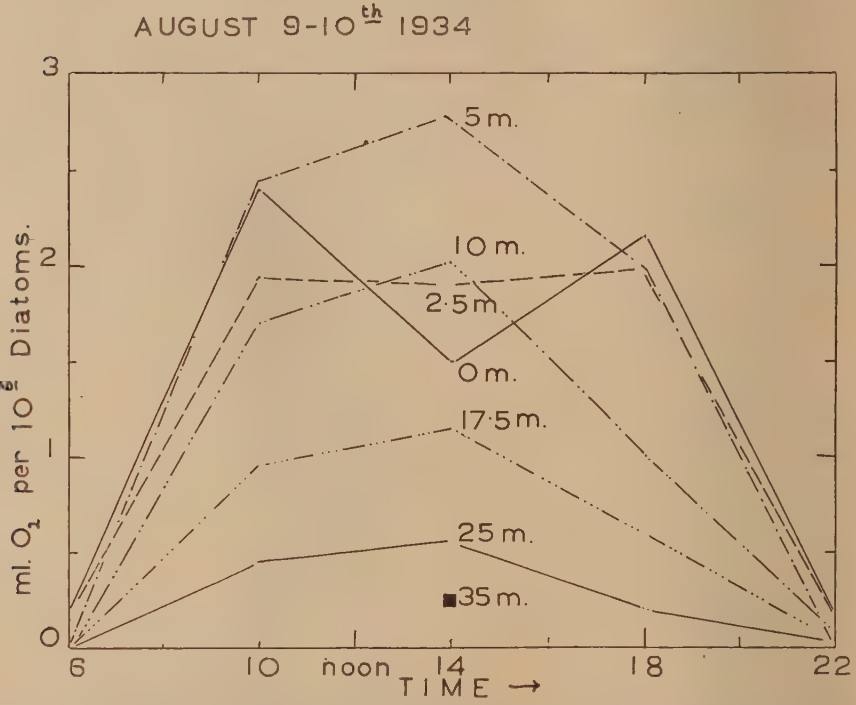


Fig. 7. Photosynthesis experiment with *Coscinodiscus* off Stoke Point on August 9–10 1934. The results of this experiment, shown in Fig. 6, are here plotted with the oxygen-production in ml. per million diatom cells as ordinates and the time of day as abscissae. The curves represent the results at each depth, as indicated. This method of showing the results is directly comparable with Marshall & Orr's figs. 7 and 10 (1928, p. 328).

The plain curve in Fig. 8 represents the energy integrals for July 12–13, plotted half-scale as compared with previous figures. The energy for the experiment on July 19–20 is shown by small circles, as the values are almost identical with those shown by the curve (see p. 309 and Table III).

The total oxygen production during the first experiment is shown by solid circles and squares, that for the second by rings and crosses. The oxygen values, like the energy values, are plotted half-scale as compared with previous figures; the relative scale of oxygen and energy in Fig. 8 is therefore unaltered.

The figure shows that a similar relation between oxygen production and energy holds good for these long exposures, as for the short exposures; but there are greater discrepancies. This is partly to be expected on account of the increased opportunity for accumulation of end-products in both diatoms and medium during the longer exposures (p. 320).

TABLE VII. PHOTOSYNTHESIS EXPERIMENTS, JULY 1934. EXPOSURE OF DIATOMS IN ROUND BOTTLES (*R*) AND FLAT BOTTLES (*F*)

		Oxygen in ml. per litre			
		July 12 and 13 2120–2100 G.M.T.		July 19 and 20 2035–1915 G.M.T.	
Depth in metres	Bottle	Light (*l*)	Dark (*d*)	Light (*l*)	Dark (*d*)
0	*R*	6·21	4·89	Lost	Lost
		6·23			
		6·21			
	F	5·95	—	—	—
		5·97			
2·75	*R*	5·76	4·88	6·02	5·04
(12th)		5·48		6·12	
2·5		5·70		6·08	
(19th)	*F*	5·83	—	5·64	—
		5·79		5·66	
5·0	*R*	6·92	4·88	6·73	5·02
		6·92		6·74	
		6·93		6·71	
	F	6·23	—	5·73	—
		6·28		5·76	
7·5	*R*	6·89	4·89	6·65	5·08
		6·70		6·66	
		6·90		6·65	
	F	6·26	—	5·69	—
		6·25		5·73	
10	*R*	6·52	4·88	6·57	5·03
		6·50	Av. 4·88	6·58	Av. 5·04
		6·52		6·55	
	F	6·15	—	5·66	—
		—		5·69	
12·5	*R*	6·36	4·89	6·49	5·05
		6·38		6·42	
		6·34		6·45	
	F	6·05	—	5·59	—
		6·06		5·57	
15	*R*	6·17	4·90	6·25	5·07
		6·25		6·29	
		6·25		6·27	
	F	5·94	—	5·55	—
		5·90		5·56	
17·5	*R*	6·39	4·88	—	—
		6·40			
		6·34			
	F	5·88	—	—	—
		5·85			
20	*R*	6·09	4·90	6·00	5·09
		6·03	Av. 4·89	5·99	
		6·08		6·01	
	F	5·72	—	5·46	—
		5·72		5·45	
25	*R*	5·89	4·91	Lost	Lost
		5·82			
		5·79			
	F	5·53	—	,,	—
		5·53			
30	*R*	5·67	4·92	—	—
		5·71	Av. 4·92		
		5·62			
	F	5·31	—	—	—
		5·30			
35	—	—	—	Lost	Lost
45	*R*	—	—	5·12	5·06
				5·14	Av. 5·07
				5·13	
	F	—	—	5·15	—
				5·16	

		Initial contents			
		O_2 (*In*)	Cells per ml.	O_2 (*In*)	Cells per ml.
0–45	*R*	4·96	150	5·12	163
		4·96	(*l*)	5·10	
		4·99	139	5·13	
		4·99	(*d*)	5·11	
0–45	*F*	4·94	108	5·18	53
		4·94		5·16	
		4·95		5·18	
				5·16	

Sunrise 0410 G.M.T. 0426 G.M.T.
Sunset 2031 ,, 2016 ,,

Apart from the irregularities in the results, especially for July 12, there remains an obvious discrepancy between the amount of oxygen produced by a million cells in similar illumination in the two experiments, that for July 12 being distinctly the greater. There is evidence that this may have been due to the size of the individual cells: first, although the cells were not measured, those in the culture for July 12 were recorded as unusually large, whereas those for July 19 were not; and, second, the average respiration rate of a million cells per hour was about 0·025 ml. for July 12 and only 0·017 ml. for July 19 at similar depths. If this be taken as indicative of the relative sizes of the cells in the two cultures, the oxygen production for July 12 can be reduced

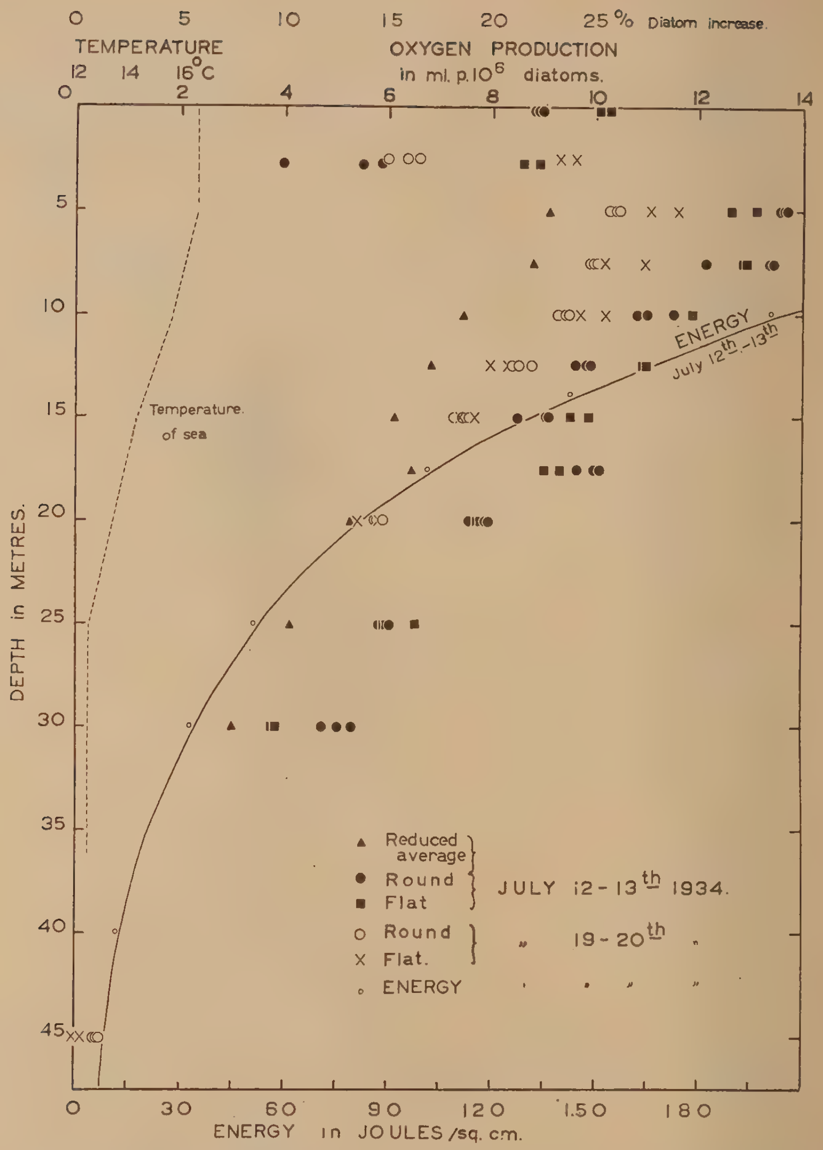


Fig. 8. Photosynthesis experiments with *Coscinodiscus* at L 5 on July 12–13 and July 19–20 1934. The exposures lasted about 24 hr. each, the first from 2120 to 2100 and the second from 2035 to 1915 G.M.T. The scales on which total oxygen production and total available energy are plotted are halved in relation to depth, as compared with Figs. 3–6, but remain the same relative to one another. The rounds and squares represent the results with round and flat bottles for July 12–13, the rings and crosses those for round and flat bottles for July 19–20. The triangles represent average values for July 12 reduced to the same level as for July 19, in accordance with respiration values (see text, p. 331). The plain curve represents the total available energy on July 12–13; the small rings indicate the closely similar values for July 19–20. The dotted curve represents the temperature of the sea on the evening of July 19.

accordingly and then compared with that for July 19. This gives the average values plotted as triangles in Fig. 8, where they show a close approximation to the values for July 19 except that the curve is slightly steeper. The latter point and the other irregularities in the results suggest that strong currents, due to the spring tide, may have been putting a heavy strain on the buoy, at least during a part of the exposure on July 12–13. This would displace the cable considerably from the vertical, and bring the cages nearer to the surface than was intended.

Near the surface the flat and partially shaded bottles again tend to show higher values for oxygen production than the clear round bottles at the same levels (p. 323).

On July 12 no cages were exposed below 30 m., but this proved unexpectedly to be well above the "Compensation Point" (p. 336), where photosynthesis just balances respiration in the 24 hr. On July 19 cages were set down to 45 m., and the bottles there showed that the oxygen production just balanced the consumption (Table VII), so that the 45 m. cage must have been close to the compensation point: unluckily the cages at 25 and 35 m. were lost, owing to bad weather, and their confirmation is therefore lacking. The corrected values for July 12 serve as confirmation as far as they go; and it is found that a similar depth for the compensation point is obtained by combining the results of the four successive exposures covering 23·5 hr. on August 9–10 1934.

The Relation of Photosynthesis to Energy in the Sea

It has been assumed, in accordance with the conclusions of Stanbury (1931, p. 651), that the energy in radiation of all wave-lengths, within the visible spectrum, may be used equally effectively by the diatoms for their photosynthesis. Hoover (1937, p. 6) has since shown that the entire visible spectrum is effective for photosynthesis by wheat seedlings, but that there is a principal maximum efficiency for equal incident energy at 6550 A. in the red, and a secondary one at 4400 A. in the blue; between these wave-lengths a fairly high level of photosynthesis is attained throughout, and outside these limits the level falls rapidly to zero.

In the English Channel radiant energy in the blue and yellow regions of the spectrum penetrates into the sea at almost the same rate as that estimated for the total energy, and the rate for green is not widely different (Fig. 1). It is, therefore, possible that the apparent correspondence, to be seen in Figs. 3–8, between oxygen production by diatoms and the total energy, might only imply a correspondence with energy in the blue, or the yellow, or the green, or any combination of these wave-lengths. At present there seems to be no evidence to decide this point; but one thing is quite certain, in the present case, and that is that the photosynthesis is not solely, nor even mainly, dependent upon energy in the red, because the red is practically extinguished within 12–15 m. from the surface of the sea, whereas the diatoms assimilate actively at depths of 40 and even 50 m. Atkins & Poole (1933, p. 156) made a similar deduction from Marshall & Orr's results in the Clyde.

Accessory yellow and brown pigments are especially abundant in red and brown algae and in diatoms, and it has frequently been suggested, though never fully substantiated, that the energy in light of complementary colour, absorbed by these pigments, may be used in photosynthesis. On the other hand, Schmucker (1930, p. 851) claimed that the energy absorbed by these pigments is thereby removed from the field of photosynthetic activity, rather than made available for it (Warburg & Negelein, 1923, p. 191). Positive evidence that yellow pigments in etiolated leaves would liberate oxygen in the light, when no chlorophyll was present, has been obtained by Smith (1930, p. 148): he also emphasized, in reviewing the chemical nature of these pigments, the ease with which many of them might apparently be formed from, or transformed into, chlorophyll. Moreover, definite colour changes have been described in diatoms by Stanbury (1931, p. 651) and in species of the blue-green alga *Oscillatoria* by Gaidukow (1903, p. 487); these changes were complementary in colour to that of the light in which the cultures were grown, and were apparently due to a greater or lesser development of brownish pigments, masking the green of the chlorophyll. It is tempting to believe that such changes are an adaptation to aid in photosynthesis, and to suppose that, if the time required for the colour change to occur were a matter of days, diatoms, growing in the sea and adapted to blue-green light by the development of brownish pigment, should be able to produce more oxygen, for a given intensity of daylight, in deep water where blue-green light predominates, than should the experimental diatoms, grown in daylight and adapted to a high proportion of red light by development of mainly the green pigments.

But it is necessary to pass on from such speculations on the wave-length of the light to the consideration of its intensity in relation to photosynthesis.

In plotting the total available energy and the oxygen production of *Coscinodiscus excentricus*, the measured or computed amounts for each exposure were shown in Figs. 3–8, as already described. The general relation between energy and oxygen production has been pointed out: there is a direct relation between the two in deep water; the oxygen reaches a maximum at about 5 m. below the surface, and usually decreases above this level, if the light is at all bright. But in the experiments so recorded the length of time for which the diatoms were exposed differed considerably; and it is clearly necessary to eliminate this time factor in order to obtain a true comparison between the different exposures. This is done in Fig. 9, where the oxygen production per hour is plotted as ordinates against the average amount of energy per hour as abscissae. For simplicity the results from each set of three bottles, similarly exposed, have been averaged.

When the flux of energy is below about 7·5 joules, or 1·8 g.-cal. per cm.^{2} per hr., there is the usual straight line relation between the energy and the oxygen production, as measured in the six short exposures in two successive

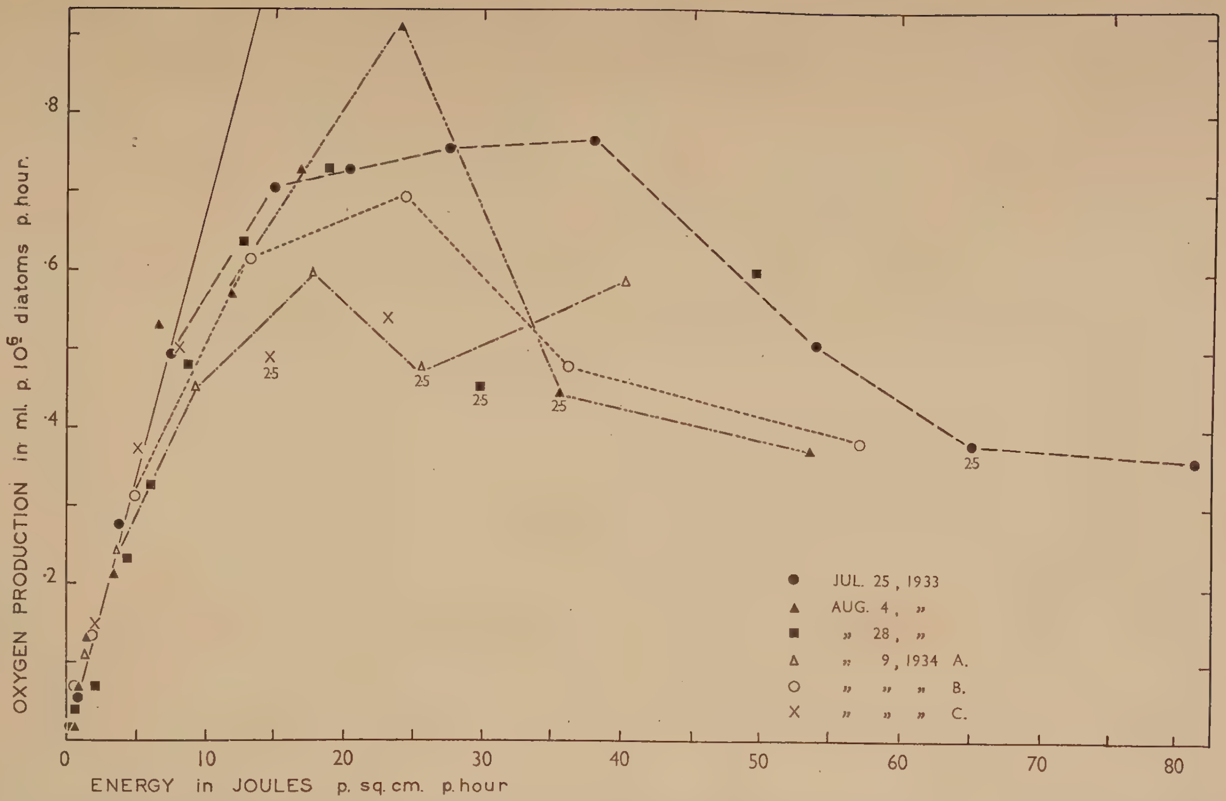


Fig. 9. The hourly oxygen production and total available energy in all short exposures in 1933 and 1934. The straight line from the origin indicates the direct relation between oxygen production and energy at intensities less than about 7·5 joules per hr. At greater intensities the relation in different experiments is indicated by broken lines. The sea was very calm, the light was very bright, and conditions were relatively constant throughout the exposure on July 25; the conditions were probably least constant on August 9. The results obtained in the cages suspended at 2·5 m. are marked 2·5 (see text, p. 335). The energy values for August 9 are derived from curves *A*, *B* and *C* × 0·66 in Fig. 6.

years (Fig. 9). It is hardly to be expected that the agreement should be more exact, considering the difficulties of work at sea, and the important fact that the energy was by no means constant at the value recorded during any one exposure. It is rather a matter for surprise that the agreement is so good, when the energy flux varied so much with the fluctuations in intensity of daylight: but it must be remembered that the energy values for August 9 are slightly magnified, relative to the rest (p. 325).

It is possible to estimate quite roughly from this straight-line relation the actual amount of energy available for absorption for a given oxygen production, and thence to calculate the "percentage utilization" of the energy (Juday & Schomer, 1935, p. 76). Assuming that the cells are so thinly scattered in the experimental bottles that none casts a shadow on any other, and that all are lying horizontally, we may estimate the area of the upper exposed surface of a million cells at about 20 cm.^{2}, if the diameter of each cell is between 50 and 60μ. At a flux of 7·5 joules the oxygen production of a million cells is about 0·5 ml. per hr.: the amount of energy available over an area of 20 cm.^{2} in 1 hr. would be 150 joules, or 300 joules for 1·0 ml. of O_2. This is equal to 72 g.-cal. If the energy required to form a gram molecule of glucose be taken as 676,000 g.-cal., and is accompanied by the liberation of 22·4 × 6 l. O_2, then the energy required for the production of 1 ml. O_2 would be about 5 g.-cal., and the utilization would amount to about 7% in those cases falling on the straight line in Fig. 9. Juday & Schomer (1935, p. 80) give the maximum utilization in their exposures as about 11%.

When the flux of energy is greater than 7·5 joules per hr., the results are less consistent, although most of them show that there is an optimum illumination for oxygen production, somewhere between 20 and 30 joules per hr. (4·8–7·2 g.-cal.), while at greater intensities there is a marked decrease in oxygen, rather than a maintenance of the optimum level as would be expected under the influence of any direct limiting factor, other than light.

The most consistent results were those obtained from the exposure on July 25 1933, when the conditions were as nearly steady as could be expected in the field: the sea was as calm as the traditional mill-pond, and the record of the illumination showed a steady curve throughout the exposure, corresponding to the cloudlessness of the sky. In this case the oxygen production curve (Fig. 9) begins to diverge from the straight line at about 10 joules per hr. (2·4 g.-cal.), rises slowly to an optimum between 20 and 40 joules per hr., falls again till the energy reaches about 60 joules per hr. (14·4 g.-cal.) and then flattens out.

The form of the curves for August 4 1933, and for period *B* on August 9 1934 (Fig. 9), are both similar to that for July 25, but the first has a higher maximum, and both show the decrease at about 25 joules instead of 40. In both the variations in energy during the exposure were much greater than on July 25, and presumably therefore included moments of much brighter illumination.

The results for the three remaining exposures, August 28 1933, and periods *A* and *C* on August 9 1934, are less regular, having aberrant low values for the bottles suspended at 2·5 m. (the same is also true to a lesser extent for August 4 and for period *B*, August 9). The same discrepancy in the 2·5 m. values can be seen in Figs. 4–8. The cage containing these bottles was suspended below the bamboo, connecting the surface cage to the buoy, and not under the buoy; for it had been found by experiment that bottles suspended at 2·5 m., under the buoy, gave distinctly higher values for oxygen production than those under the bamboo. It was concluded that shading by the buoy reduced the usual inhibitory effect of the strong light near the surface, and that the bottles under the bamboo were therefore giving the truer value. It is difficult to account for these bottles showing greater inhibition than those at the surface; but it is important to notice that these aberrant values occurred on the rougher days. It is perhaps plausible to suggest that passing waves alternately cast shadows and focused bright shafts of light upon these bottles, so that they had intervals of exposure to very much brighter illumination than the average value shown for the energy in Fig. 9.

Inhibition of photosynthesis in bright light (p. 323) has been frequently recorded for shade plants (e.g. Montfort & Neydel, 1928, p. 812), and those aquatic plants which are also adapted to low light intensities (e.g. *Elodea*: Ruttner, 1926, pp. 14 and 21; green algae: Juday & Schomer, 1935, p. 79; Curtis & Juday, 1937, p. 125; and diatoms: Gaarder & Gran, 1927, p. 37, Table 6; Marshall & Orr, 1928, p. 325; and Jenkin, 1930, p. 34). The nature of the inhibition and its relation to the intensity of the light does not seem to have been fully elucidated; but it is probable that several factors may be involved, including the rearrangement or contraction (systrophe) of chloroplasts, the accumulation of end-products (Schreiber, 1927, p. 12), and death of increasing numbers of cells after prolonged exposure to very bright light.

The results on July 25 1933 might be accounted for, in part at least, by systrophe; in that case, the contraction of the chloroplasts might be supposed to have begun at an energy flux of about 40 joules or 9·6 g.-cal. per hr., causing a marked fall in the rate of photosynthesis; the contraction would have reached its limit by 60 joules per hr., and would then act as a direct "limiting factor" at all higher illumination intensities, in which the oxygen production remains at a constant level. Similarly, for the other short exposures, although the average light intensity was below the threshold for inducing systrophe, yet the occasional exposures to high intensity that occurred might be sufficient to induce and maintain systrophe as a limiting factor for most of the time.

In any case, interesting results might be expected from a fuller investigation of such material as *Coscinodiscus excentricus*, with its well-marked inhibition at illumination intensities (e.g. 10 g.-cal. per cm.^{2} per hr.) so much below those of full daylight. This species may well be contrasted with the shallow-water diatoms reported by Curtis & Juday (1937, p. 131) as giving their maximum yield of oxygen at the surface of a freshwater lake, where the energy flux was 60 g.-cal. per cm.^{2} per hr.

Turning from the maximum energy flux, in which photosynthesis can continue, to the minimum leads to a consideration of the "Compensation" value. Here there are really two distinct conceptions to be found in previous work: the first is the conception of an intensity of light, or energy, which is sufficient to maintain the *status quo*, so that the plant's oxygen production by photosynthesis will exactly balance its oxygen consumption by respiration during the few hours of the investigation; the second is the conception of an intensity of light which is economically sound, so that the plant's oxygen production by photosynthesis during the hours of daylight would be sufficient to balance the consumption during the whole 24 hr. The first of these may conveniently be called the "compensation intensity" (Pettersson *et al.* 1934, p. 4) and the second the "compensation point" (Marshall & Orr, 1928, p. 324). It is clear that the illumination at the "compensation point" must be greater than at the "compensation intensity"; yet it is the minimum at which the plant in question could survive in nature, and is still too low to allow for any increase in crop.

The compensation intensity cannot be as accurately derived from the present results as from those of Pettersson and others (1934, p. 4), since the exposures were not designed to that end. The energy in the illumination at the compensation point, however, can be ascertained from the 24 hr. exposures of *Coscinodiscus*. On July 19–20 1934, the bottles, in which compensation occurred in just under 24 hr., received 9 joules per cm.^{2} during the exposure. Since daylight lasted for about 16 hr. out of the 24, the average energy flux at the compensation point was 0·55 joule or 0·13 g.-cal., per cm.^{2} per hr. This is equivalent to the energy in visible daylight of an intensity of about 360 lux.

Pettersson and his colleagues (1934, p. 4) found the compensation intensity for mixed plankton in the Gullmar Fjord to be about 400 lux, and this has since been confirmed by Höglund & Landberg (1936, p. 33). The intensities found by two such different methods as theirs and mine are remarkably similar, when it is remembered that although the compensation intensity is naturally lower than the compensation point, yet their intensity would tend to be higher than mine because their estimation of respiration included that of the animals in the samples as well as that of the phytoplankton.

Schreiber (1927, p. 12) found the compensation point for *Biddulphia mobiliensis* to be as low as 100 lux, using constant artificial light, but he also found the optimum for this species to be no more than 800 lux or about 0·5 g.-cal. These values, however, are not strictly comparable with those obtained in the sea because of the differences in the spectral distribution of the energy in natural and artificial light.

Schomer & Juday (1935, p. 187) found higher intensities of energy at the compensation point for green algae in some Wisconsin lakes, varying from 0·25 to 0·95 g.-cal. per cm.^{2} per hr.

Unfortunately no direct comparison can be made with Clarke & Oster's (1934, p. 72) measurements of light intensity at Wood's Hole and in the Gulf of Maine, since they give their results for certain blue and red regions of the spectrum only.

Further measurements of available submarine energy will almost certainly bring into line the apparently discordant results which have so far been recorded as to the depth at which compensation occurs in the sea; for these depths vary from close to the surface in the Clyde in winter (Marshall & Orr, 1928, p. 341) to 45 m. in the English Channel in summer (Fig. 8) or 50 m. in the Gulf of Maine (Clarke & Oster, 1934, p. 72); probably even greater depths would be found in the very transparent waters of the Mediterranean or open Atlantic. The differences in depth are almost certainly due to differences in transparency and in colour of the water in these different localities, as well as to differences in the intensity of the incident light at the time of the investigation. Marshall & Orr (1928, p. 325) have already pointed out the effect of the lower intensity of winter daylight and of reduced transparency in spring, which they attribute to diatoms, in bringing the depth of compensation nearer to the surface than it is at midsummer. Reduced transparency, due to silt, could easily account for the fact that, in the shallow waters of Frederikshavn, Nielsen (1932, p. 6) found the compensation point for samples of mixed plankton at depths between 4·5 and 7 m. It certainly does not seem necessary to postulate, as he does, that, because Marshall & Orr found the compensation point as deep as 30 m., his plankton was adapted to brighter light than theirs. Just as great differences in the depth of the compensation point are indicated elsewhere; calculating from photo-electric measurements (Atkins & Poole, 1933, fig. 7, p. 147), the energy at 20 m. in the open water of the English Channel, for instance, is twice that in the inshore waters of Whitsand Bay; and in the Gulf of Maine the transparency is three times that of Wood's Hole Harbour (Clarke & Oster, 1934, p. 72).

Changes in the depth at which the compensation intensity occurs, following changes in the intensity of the incident daylight, were well shown by Pettersson and others (1934, p. 14), for in an extreme case they had to move their samples from 19 m. to the surface (April 17) in order to keep them at a light intensity of 400 lux throughout the exposure. Incidentally, the colour of the illumination would inevitably change considerably between 19 m. and the surface (cf. Fig. 1), so that their plankton was not exposed to similar illumination throughout the time, even if the energy flux were maintained constant.

A rough estimate of the rate of growth of *Coscinodiscus* under optimum light conditions may be gained from the results of the 24 hr. exposures. The optimum energy flux occurred at about 10 m. below the surface, and amounted, on the average, to 13 joules or 3·1 g.-cal. per cm.^{2} per hr., during the hours of daylight. In the 24 hr. on July 12–13 the number of cells per unit volume increased from 95 (±3) to 120 (±4); this was equivalent to a 25%

increase in crop (Fig. 8). This estimate is confirmed by analyses of the phosphorus in the diatoms showing an increase from 80 to 100 μg. per million cells (Cooper, Appendix to this paper, Table A).

Analyses of samples of the same culture of diatoms as that used on July 12 (see Appendix) gave 0·08 mg. phosphorus and 0·44 mg. nitrogen per million cells; the oxygen production for a million cells, corresponding to the 25 % increase, was 10–12 ml.; thence, assuming a 1 : 1 ratio between oxygen produced and carbon dioxide assimilated, it may be calculated that the original million cells contained about 2·5 mg. carbon. This gives a ratio for C : P : N of 32 : 1 : 5·5, which may be compared with a typical analysis for fresh* diatoms by Brandt & Raben (1919–22, p. 208) giving a ratio for C : P : N : Fe of 33 : 1 : 5·6 : 2·0.

The ratio of iron to phosphorus in the present cultures was according to Cooper (Appendix, p. 343) at most 1·3 : 1.

An interesting speculation on crop production in the sea in relation to seasonal changes in illumination has also been based on the results of my 24 hr. exposures by Harvey, Cooper, Lebour & Russell (1935, p. 412). They point out that in winter the average amount of light reaching the surface of the sea in a day would be about one-ninth of that in a summer day, so that the total energy available in the sea in the winter would be equal to that below 16 m. in the summer exposure (Fig. 8); there should therefore be no inhibition of photosynthesis in the winter. In fact, allowing even for the effect of winter temperatures, the oxygen production by diatoms behaving like *Coscinodiscus* should only be reduced to one-fourth by the reduction of light to one-ninth. Moreover, there would be less limitation of the natural crop production by shortage of nutrient materials in the sea in winter and early spring, so that the production should be proportionately higher than would be expected from a consideration of the light alone.

There would probably always be a greater shortage of nutrient materials in the sea, than under the experimental conditions, so that the picture of the possible productivity derivable from the present results could rarely, if ever, be realized in nature. Nevertheless, the results serve to show, for *Coscinodiscus*, the nature and extent of the limitations that are set upon photosynthesis by the light in the natural environment.

Some experiments were also made with *Biddulphia regia*, which was found to behave in just the same way as *Coscinodiscus* and to have a similar optimal illumination intensity. Both these species, however, were being used for experiments in the summer, whereas, normally, they are only abundant in the sea in winter or early spring. It is obviously desirable, therefore, to compare the behaviour of such species with that of some summer diatom; the only relevant information for marine diatoms seems to be the observation of Marshall & Orr (1928, p. 337) that the optimum light intensity was the same for a summer species of *Chaetoceros* as for the winter species, *Coscinoscira polychorda*, with which they carried out the majority of their experiments.

---

* Their analyses on samples preserved in alcohol are not reliable owing to the loss of phospholipins in solution.

In conclusion, it may be said that the present method seems unlikely to yield much further information, at least in a place like Plymouth. It is extremely laborious; the distance of the open water from the Laboratory makes it slow; and the exposure to the Atlantic reduces the accuracy of the work done on board ship, as well as the accuracy of the depth at which the samples are suspended. In addition to these specific difficulties there remains the natural variability of daylight, which precludes, at least in the English climate, any really accurate results such as are obtainable under laboratory conditions.

The greatest scope for future work would seem to lie in the laboratory, where the diatoms could be exposed to constant light and temperature: then it should be possible to compare the oxygen production due to light of equal energy content but of different wave-lengths, and also to compare the productivity of different species of diatoms exposed to similar lighting.

Coscinodiscus excentricus has many characters which should recommend it for further work; its symmetrical and compact form and the ease with which it grows under laboratory conditions have already been referred to. In common with other diatoms it presumably shows the colour adaptations which require further elucidation. Last, but not least, it can carry out its photosynthesis in light of very low intensity; it should therefore be possible to supply it with light of sufficient intensity in quite restricted regions of the spectrum, if not actually with monochromatic light, in order to compare the efficiency of radiant energy of different wave-lengths, and to investigate the nature of the inhibition of photosynthesis by relatively bright light.

ACKNOWLEDGEMENTS

I have great pleasure in thanking Dr E. J. Allen, F.R.S., for his personal instruction and encouragement in the making of many diatom cultures, and for the facilities of the Plymouth Laboratory, during the successive tenures of the Ray Lankester Investigatorship, a grant from the Stuart Research Fund of Newnham College, and a grant made through Prof. Stanley Gardiner, F.R.S.; I was also given the use of the Cambridge Table at Plymouth in 1934, and the British Association Table in 1935.

I most gladly and gratefully acknowledge my indebtedness to both Dr W. R. G. Atkins, F.R.S., and Dr H. H. Poole for supplying me with data on light and energy. I also wish to thank Dr L. H. N. Cooper for his help with oxygen estimations as well as in the arduous experiment of August 9–10 1934, when he, Dr L. E. Bayliss, and Mr G. I. Crawford combined to take shifts on the trawler for me. Nor can I end my acknowledgements without thanking Capt. Lord and the crew of the M.B.A. steam trawler *Salpa*, without whose skilful handling of the gear the results described in this paper could never have been secured.

SUMMARY

1. A method, due to Poole & Atkins, is described for computing the total available energy at any depth in the sea, in joules or g.-cal.

2. The oxygen production of pure cultures of the diatom *Coscinodiscus excentricus* Ehr. was measured by the Winkler method after exposure of the diatoms in bottles at known depths in the sea.

3. The results of simultaneous measurements of oxygen production and of energy are given for 6 days in July and August 1933 and 1934.

4. Factors, other than light, that might affect the rate of oxygen production in the experiments are discussed and shown to be negligible. It is assumed that diatoms can use energy for photosynthesis equally well in all parts of the visible spectrum.

5. When the energy flux during the exposures is less than 7·5 joules or 1·8 g.-cal. per cm.^{2} per hr., the oxygen production is directly proportional to the energy. The utilization of the available energy then amounts to about 7%.

6. When the energy flux is greater than 7·5 joules per cm.^{2} per hr. the oxygen production is gradually inhibited, but the results are less consistent. The nature of this inhibition, and the causes of the irregularity in the results are discussed. Systrophe appears to be induced by an energy flux of about 40 joules, or 9·6 g.-cal., per cm.^{2} per hr.

7. The energy flux at the "compensation point" is found to be 0·55 joule or 0·13 g.-cal. per cm.^{2} per hr. This is compared with the results of previous workers.

8. Compensation in the clear, open water of the English Channel in summer occurred at a depth of about 45 m.

9. Analyses of the diatoms, based partly on the data in Cooper's Appendix (p. 343), gave a ratio of C : P : N of 32 : 1 : 5·5. The ratio for Fe : P was about 1 : 1.

10. Similar results were obtained with *Biddulphia regia* M. Schultze.

REFERENCES

ABBOT, C. G., 1929. Optical Society of America Committee, on "The Unit of Photographic Intensity". Quoted in *7th Int. Congr. Photogr. London*, pp. 152–61.

ALLEN, E. J. & E. W. NELSON, 1910. On the artificial culture of marine plankton organisms. *Journ. Mar. Biol. Assoc.*, Vol. VIII, pp. 421–74.

ATKINS, W. R. G., 1923. The silica content of some natural waters and of culture media. *Journ. Mar. Biol. Assoc.*, Vol. XIII, pp. 151–9.

ATKINS, W. R. G. & H. H. POOLE, 1930. The photo-electric recording of daylight. *Nature*, Lond., Vol. 125, pp. 305–6.

—— —— 1931*a*. Photo-electric measurements of illumination in relation to plant distribution. Pt. 4. *Sci. Proc. R. Dublin Soc.*, Vol. 20 (4), pp. 13–48.

—— —— 1931*b*. A preliminary comparison of the neon-lamp and potentiometer methods of submarine photo-electric photometry. *Journ. Mar. Biol. Assoc.*, Vol. XVII, pp. 617–31.

ATKINS, W. R. G. & H. H. POOLE, 1933. The photo-electric measurement of the penetration of light of various wave-lengths into the sea and the physiological bearing of the results. *Phil. Trans. Roy. Soc.*, B, Vol. 222, pp. 129–64.

—— —— 1936*a*. The photo-electric measurement of the diurnal and seasonal variations in daylight and a globe integrating photometer. *Phil. Trans. Roy. Soc.*, A, Vol. 235, pp. 245–72.

—— —— 1936*b*. Photo-electric measurements of the luminous efficiency of daylight. *Proc. Roy. Soc.*, B, Vol. 121, pp. 1–17.

BLACKMAN, F. F., 1905. Optima and limiting factors. *Ann. Bot.*, Vol. 19, pp. 281–95.

BRANDT, K. & E. RABEN, 1919–1922. Zur Kenntnis der chemischen Zusammensetzung des Planktons und einiger Bodenorganismen. *Wiss. Meeresuntersuch. Abt. Kiel*, Bd. XIX, pp. 175–210.

BUCH, K., H. W. HARVEY, H. WATTENBERG & S. GRIPENBERG, 1932. Über das Kohlensäuresystem im Meerwasser. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. LXXIX, pp. 8–70.

CLARKE, G. L., 1933. Observations on the penetration of daylight into mid-atlantic and coastal waters. *Biol. Bull.*, Vol. 65 (2), pp. 317–37.

CLARKE, G. L. & R. H. OSTER, 1934. The penetration of the blue and red components of daylight into Atlantic coastal waters and its relation to phytoplankton metabolism. *Biol. Bull.*, Vol. 67 (1), pp. 59–75.

CURTIS, J. T. & C. JUDAY, 1937. Photosynthesis of algae in Wisconsin lakes. III. Observations in 1935. *Int. Rev. Hydrobiol.*, Bd. 35, pp. 122–33.

GAARDER, T. & H. H. GRAN, 1927. Investigations of plankton in the Oslo Fjord. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. XLII, pp. 3–48.

GAIDUKOW, N., 1903. Weitere Untersuchung über den Einfluss farbigen Lichtes auf die Färbung der Oscillarien. *Ber. Dtsch. Bot. Ges.*, Bd. XXI, pp. 484–92.

HARDER, R., 1921. Kritische Versuche zu Blackmans Theorie der „begrenzenden Faktoren" bei der Kohlensäureassimilation. *Jahrb. Wiss. Bot.*, Bd. 60, pp. 531–71.

HARVEY, H. W., 1934. Measurement of phytoplankton population. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 761–73.

HARVEY, H. W., L. H. N. COOPER, M. V. LEBOUR & F. S. RUSSELL, 1935. Plankton production and its control. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 407–42.

HÖGLUND, H. & S. LANDBERG, 1936. Further investigations upon the photosynthesis of phyto-plankton by constant illumination. *Rapp. Proc. Verb. Cons. Int. Explor. Mer*, Vol. XCV, pp. 32–3.

HOOVER, H. W., 1937. The dependence of carbon dioxide assimilation in a higher plant on wave-length of radiation. *Smithson. Misc. Coll.* Vol. 95 (21), pp. 1–13.

JENKIN, P. M., 1930. A preliminary limnological survey of Loch Awe (Argyllshire). *Int. Rev. Hydrobiol.*, Bd. 24, pp. 24–46.

JUDAY, C. & H. A. SCHOMER, 1935. The utilization of solar radiation by algae at different depths in lakes. *Biol. Bull.*, Vol. 69 (1), pp. 75–81.

LEBOUR, M. V., 1929. *The Planktonic Diatoms of Northern Seas.* Ray Soc. Lond.

MARSHALL, S. M. & A. P. ORR, 1928. The photosynthesis of diatom cultures in the sea. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 321–60.

MONTFORT, C. & K. NEYDEL, 1928. Zur Beurteilung der „Inaktivierung" u. des „Zeitfaktors" der Lichtwirkung bei der Assimilation Stomata-freier Schatten-Farne. *Jahrb. Wiss. Bot.*, Bd. 68, pp. 801–43.

NIELSEN, E. STEEMANN, 1932. Einleitende Untersuchungen über die Stoffproduktion des Planktons. *Medd. Komm. Havundersøg. Kbh.* Ser. *Plankton*, Vol. II (4), pp. 3–14.

PETTERSSON, H., 1934. A transparency-meter for sea water. *Göteborg Vetensk. Samh. Handl.*, 5. B, Bd. 3 (8), pp. 3–17.

PETTERSSON, H., H. HÖGLUND & S. LANDBERG, 1934. Submarine daylight and the photosynthesis of phyto-plankton. *Göteborg Vetensk. Samh. Handl.*, 5. B, Bd. 4 (5), pp. 3–17.

POOLE, H. H. & W. R. G. ATKINS, 1926. On the penetration of light into sea-water. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 177–98.

—— —— 1928. Further photo-electric measurements of the penetration of light into sea water. *Journ. Mar. Biol. Assoc.*, Vol. XV, pp. 455–83.

—— —— 1929. Photo-electric measurements of submarine illumination throughout the year. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 297–324.

—— —— 1933. Experiments on the suitability of some rectifier photo-electric cells for the measurement of daylight. *Sci. Proc. R. Dublin Soc.*, Vol. 20 (36), pp. 537–46.

—— —— 1934. The use of a selenium rectifier photo-electric cell for submarine photometry. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 727–36.

—— —— 1935. The standardisation of photo-electric cells for the measurement of visible light. *Phil. Trans. Roy. Soc.* A, Vol. 235, pp. 1–27.

—— —— 1936. The standardisation of photo-electric cells for the measurement of energy. *Sci. Proc. R. Dublin Soc.*, Vol. 21 (38), pp. 363–79.

RUTTNER, F., 1926. Über die Kohlensäureassimilation einiger Wasserpflanzen in verschiedenen Tiefen des Lunzer Untersees. *Int. Rev. Hydrobiol.* Bd. 15, pp. 1–30.

SCHMUCKER, TH., 1930. Über Assimilation der Kohlensäure in verschiedenen Spektralbezirken. *Jahrb. Wiss. Bot.*, Bd. 73, pp. 824–53.

SCHREIBER, E., 1927. Die Reinkultur von marinen Phytoplankton, und deren Bedeutung für die Erforschung der Produktionsfähigkeit des Meerwassers. *Wiss. Meeresuntersuch. Abt. Helgoland*, Bd. XVI (10), pp. 1–34.

SCHOMER, H. A. & C. JUDAY, 1935. Photosynthesis of algae at different depths in some lakes of northeastern Wisconsin. *Trans. Wis. Acad. Sci. Lett.* Vol. 29, pp. 173–93.

SMITH, J. H. C., 1930. The yellow pigments of green leaves; their chemical constitution and possible function in photosynthesis. In *Contrib. Mar. Biol. Stanford Univ. Press Cal.* pp. 145–60.

SPOEHR, H. A., 1926. *Photosynthesis.* New York, U.S.A. pp. 13–393.

STANBURY, F. A., 1931. The effect of light of different intensities, reduced selectively and non-selectively upon the rate of growth of *Nitzschia closterium. Journ. Mar. Biol. Assoc.*, N.S. Vol. XVII, pp. 633–53.

WALSH, J. W. T., 1928. Artificial daylight. *Journ. Sci. Instrum.* Vol. 5, pp. 81–8.

WARBURG, O. & E. NEGELEIN, 1923. Über den Einfluss der Wellenlänge auf der Energieumsatz bei der Kohlensäureassimilation. *Z. Phys. Chem.*, Bd. 106, pp. 191–218.

APPENDIX

DETERMINATIONS OF THE PHOSPHORUS AND NITROGEN IN *COSCINODISCUS EXCENTRICUS* EHR.

By L. H. N. Cooper, Ph.D., F.I.C.

Sufficient of the culture grown as described by Miss Jenkin was placed in a stone jar and mixed thoroughly by aeration. Aliquot parts were syphoned off and filtered through a silk disk having 200 meshes to the linear inch. Since part of the culture passed through the disk, counts were made on the medium both before and after filtration, the difference giving the number of diatoms retained by the filter and analysed for phosphorus and iron and nitrogen as described elsewhere (Cooper, 1934,* p. 755; 1935†, p. 427). The experimental data are recorded in Table A. The sampling procedure was not entirely satisfactory in dealing with culture 81 J. 13, and the concordance between duplicates is not as good as could be wished. As a weighted mean value one million cells contain 82 μg. P and 490 μg. N; but, since the cell volume in different cultures varies considerably, the best basis on which to express results is per ml. of cell matter. Each ml. of cell matter contains 23 μg. P and 120 μg. N. The ratio of nitrogen to phosphorus shown by the last two experiments is 5·5 when each is expressed in grams weight, or 12·2 when expressed as milligram-atoms.

TABLE A. ANALYSES OF *COSCINODISCUS EXCENTRICUS*

Culture	10^6 cells contain			Numerical ratio N : P	Ratio Fe : P	Volume of 10^6 cells in ml.	1 ml. of cell matter contains	
	P μg.	N μg.	Fe μg.				P μg.	N μg.
81 J. 13	79	611[1]	66	7·7	0·9	3·7	21·3	165[1]
	98	748[1]	124	—	1·3	—	26·5	202[1]
83	77	435	36	5·42	0·5	3·9	19·9	112
	—	403	—	—	—	—	—	104
81	80	440	94·5	5·50	1·2	3·3	24·2	133
81, after 24 hr. at sea	*ca.* 100							
Weighted mean	82	490	—	5·5	—	—	23	120

[1] Counts on the filtrates from these samples are lacking and the N content of 10^6 cells may be high.

The iron analyses are very discordant and at the time this was thought to be due to contamination, which would lead to the ratio of iron to phosphorus being unduly high. Later work (Cooper,† 1935, p. 429) on diatom catches taken from the sea showed clearly that the ratio Fe : P in such catches was still higher, about 4 : 1.

Harvey (1937)‡ has now shown that this 4 : 1 ratio does not measure the relative requirements of iron and phosphorus for growth of diatoms. Much of the iron appears to be adsorbed on their surface as colloidal hydroxide or phosphate. His experiments with *Nitzschia closterium* suggest that the true ratio, on a weight basis, of iron to phosphorus required for growth is 1 : 175 or less. Analyses had shown that 250 mg. P and only 5 mg. Fe or thereabouts per cu. m. had been removed from a culture medium by growing *C. excentricus* (p. 312), giving a ratio of around 1 : 50. These results, inexplicable at the time the experiments were made, fit well with the views now put forward by Harvey and suggest further that the apparent lack of agreement amongst the iron analyses in Table A was due, not to contamination, but to varying amounts of adsorbed iron.

---

* Cooper, L. H. N., 1934. The determination of phosphorus and nitrogen in plankton. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 755–60.

† Cooper, L. H. N., 1935. Iron in the sea and in marine plankton. *Proc. Roy. Soc.* B, Vol. 118, pp. 419–38.

‡ Harvey, H. W., 1937. The supply of iron to diatoms. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 205–25.

THE STRUCTURE AND FUNCTION OF THE TUBE FEET IN CERTAIN ECHINODERMS

By J. E. Smith, Ph.D.

Department of Zoology, University, Sheffield

(Text-figs. 1–8)

CONTENTS

	PAGE
Introduction and Methods	345
The Tube Feet of Ophiuroids	346
Ophiothrix fragilis (Abildgaard)	346
Ophiocomina nigra (Abildgaard)	348
Ophiura texturata Lamarck	349
The Tube Feet of Asteroids, Echinoids and Holothurians (*Marthasterias glacialis* (L.), *Echinus esculentus* L., and *Cucumaria lactea* (Forbes))	349
Adhesion and Locomotion in Asteroids, Echinoids and Holothurians	353
Adhesion and Locomotion in Ophiuroids	354
Conclusion and Summary	356
References	357

Introduction and Methods

It is well known that the suckers of the tube feet of asteroids, echinoids and holothurians serve as organs of adhesion, and that where the sucker is but poorly developed, as, for example, in *Astropecten*, which burrows in sand, adhesion is of secondary importance only. Paine (1926) has analysed the process of adhesion in the starfish *Asterias vulgaris*—a form with well-developed suckers—and concludes that adhesion is due in part to suction but "that some other factor, very probably stickiness", must also be considered.

In order to determine to what extent mucus glands may be regarded as providing means of adhesion in the Eleutherozoa as a whole, observations have been made on the tube feet of *Marthasterias glacialis*, *Echinus esculentus*, *Cucumaria lactea*, and three ophiuroids which are of common occurrence around the coasts of Britain, namely, *Ophiothrix fragilis*, *Ophiocomina nigra* and *Ophiura texturata*. Observations on living animals were made at various times during the years 1936 and 1937 in the Laboratory of the Marine Biological Association at Plymouth. Material for sectioning has been fixed in Heidenhain's "Susa" fixative in sea water, with subsequent decalcification in a 3 % mixture of nitric acid in 70 % alcohol. Sections cut 6μ thick were stained with Mallory's triple stain, Heidenhain's iron-alum haematoxylin, Delafield's haematoxylin and eosin, Giemsa, Mayer's mucicarmine and muchaematein.

I am indebted to the University of Sheffield for the use of their table at the Plymouth Laboratory and to the Director and Staff of the Laboratory for the assistance which they have afforded me during my occupation of the table.

The Tube Feet of Ophiuroids

Ophiothrix fragilis (Abildgaard).

The tube feet of an active *Ophiothrix fragilis* are maintained in a state of extension. They are long and mobile and of a length slightly greater than the width of the arm. When the animal is moving over a horizontal surface the feet are held out laterally, and frequently bend dorsally so as to arch over towards the aboral side of the arm. In so doing they provide, as far as it is possible to observe, the only means of contact with the substratum.

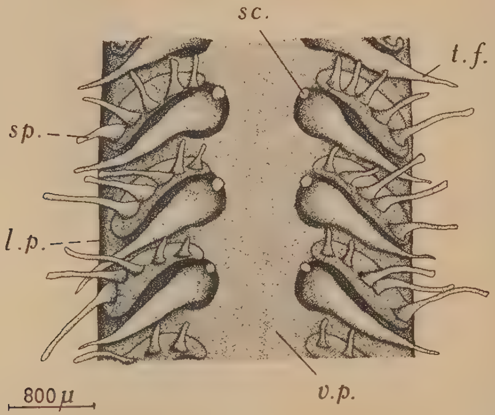


Fig. 1. A part of the oral surface of an arm of *Ophiothrix fragilis*. *l.p.*, lateral arm plate; *sc.*, tentacle scale; *sp.*, arm spine; *t.f.*, tube foot; *v.p.*, ventral arm plate.

Fig. 1 is a view of the under surface of a part of an *Ophiothrix* arm. The tube feet (*t.f.*) emerge through openings between the ventral (*v.p.*) and lateral arm plates (*l.p.*), and each is covered, proximally, by a tentacle scale (*sc.*) which, however, is minute and in no way impedes the movement of the podium.

Fig. 5 *a* represents, diagrammatically, a longitudinal section through the protruded portion of the tube foot. The epithelium (*e.*) is thrown into broad-based conical folds or "papillae" (*p.*) and is everywhere covered by a thin cuticle not exceeding 1μ in thickness. Below the epithelium there is a neurofibrillar plexus (*n.f.*), and below this again, in order, are layers of connective tissue (*c.t.*), longitudinal unstriped muscle fibres (*l.m.*) and coelomic epithelial cells (*c.e.*), the latter frequently, in fixed podia, completely obliterating the coelomic cavity. The connective tissue layer is not wholly internal to the subepithelial nerve plexus but lies, in part, external to it, a condition which is peculiar to *Ophiothrix* and is not to be found either in the Asteroidea, Echinoidea or in the other two ophiuroids studied. The podium tapers, distally, to a point, there being no trace of a sucker.

Examination of a papilla shows that it is crowded with elements which stain readily with acid fuchsin and Giemsa, rather less so with Delafield's haematoxylin and Heidenhain's iron-alum haematoxylin. Hamann (1889), in his excellent account of the nervous system of *O. fragilis*, described these papillae as sense buds and the deeply staining elements as sense cells. Each of these so-called sensory cells has a peripheral projection (Stäbchen), an elongate cell body with a nucleus and a nerve fibril directed into the subepithelial neurofibrillar plexus. Hamann is in error in his conception of the papillae as being exclusively sensory. Sensory elements there certainly are within the papilla, but the elements he described are glandular and not nervous in function.

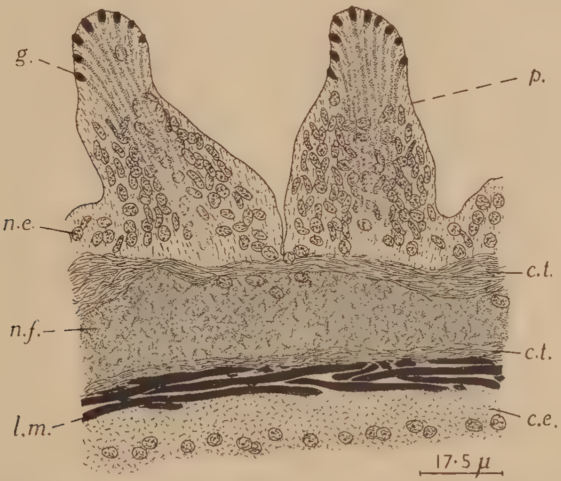


Fig. 2. A part of the wall of a tube foot of *Ophiothrix fragilis*, showing two papillae with the glandular elements. *c.e.*, coelomic epithelium; *c.t.* connective tissue; *g.*, gland; *l.m.*, longitudinal muscle fibre; *n.e.*, nucleus of epithelial cell; *n.f.*, neurofibrillar plexus; *p.*, papilla.

Fig. 2 shows two adjacent papillae in more detail. The glands (*g.*) are long and narrow, attaining to a length of 50–60μ, but of greatest width not exceeding 2μ. The base of the gland is narrower than its distal extremity and rests on the connective tissue (*c.t.*) external to the neurofibrillar plexus (*n.f.*). The long axes of the glandular elements are directed along the length of the papilla (*p.*) and either continue on this course to open terminally on the papilla or bend slightly outwards to have a subterminal opening. In sections of tube feet which have been stained with Delafield's haematoxylin or with Heidenhain's iron-alum haematoxylin, the glands are stained but feebly. In this condition they take on a uniform blue or dark grey colour and might easily be mistaken for sensory elements, but with Mallory's triple stain or with Giemsa a totally different picture is obtained. The greater part of the gland is filled with small droplets which give to it a granular appearance. The droplets situated near the base of the cell are only slightly tinged, but the colour is intensified towards the middle region. Distally, the droplets react even more readily with the stain and at the extreme tip of the gland they merge together, the whole of the tip thus being filled with a brightly staining fluid. The tip projects slightly beyond the limit of the ectoderm and apparently penetrates the thin cuticle to open on its outer surface. The nucleus of the gland cell is not distinguishable from the nuclei of the epithelial cells (*n.e.*), but in most instances appears to be applied to the middle of the gland. The papillar glands of *Ophiothrix* with their content of secretion droplets recall the "Körnchendrüsenzellen" of asteroids (Smith, 1937), but the goblet cells which occur in the latter group appear to be absent from the ectoderm of *Ophiothrix*. The goblet cells of asteroids are mucus cells, but the "Körnchendrüsenzellen" are not usually regarded as mucus secreting. In the absence of other types of glands, in the ophiuroid, one must naturally suppose that the papillar glands function as mucus cells. With Mayer's mucicarmine the glandular elements tinge only very faintly pink, but they react more readily with muchaematein. An attempt was made to test for mucus by permitting active *Ophiothrix* to walk over cover-slips which were then placed in Heidenhain's "Susa" fixative, washed and stained with mucicarmine and muchaematein. The results were entirely negative. Similar tests with *Ophiocomina*, however, showed the presence of slight traces of mucus, and when the animal was allowed to crawl up a vertical glass surface distinct tracts of mucus were to be seen where the feet had adhered to the glass. As the glands in the tube foot of *Ophiocomina* present a precisely similar appearance to those of *Ophiothrix* we may assume that both are mucus secreting.

Ophiocomina nigra (Abildgaard).

The tube feet of this ophiuroid are capable of considerable extension. When the animal is moving they are in constant motion and are never bent over the aboral surface in the manner characteristic of *Ophiothrix*. The podia emerge in pairs from apertures situated lateral to the ventral arm plates (Fig. 3, *t.f.*, *v.p.*), the apertures being partly covered, proximally, by two tentacle scales (*sc.*). The feet are papillated, though not so obviously as are the podia of *Ophiothrix*. The distal end of the tube foot does not taper to a point but ends in a blunt knob, rather like a rudimentary sucker (Fig. 5 *b*, *k.*). In the arrangement of the layers of its wall the podium differs but little from that of *Ophiothrix*; the subepithelial plexus is, however, entirely external to the connective tissue layer. The glandular elements are histologically similar to those of *Ophiothrix* and have the same staining reactions. As in the latter type, the glands are restricted to the papillar areas, but in *Ophiocomina nigra* the terminal knob, which is not represented in the *Ophiothrix* podium, is also plentifully supplied with glands which, on account of the relatively great depth of the ectoderm in this region, are correspondingly elongate, their basal ends resting against the connective tissue.

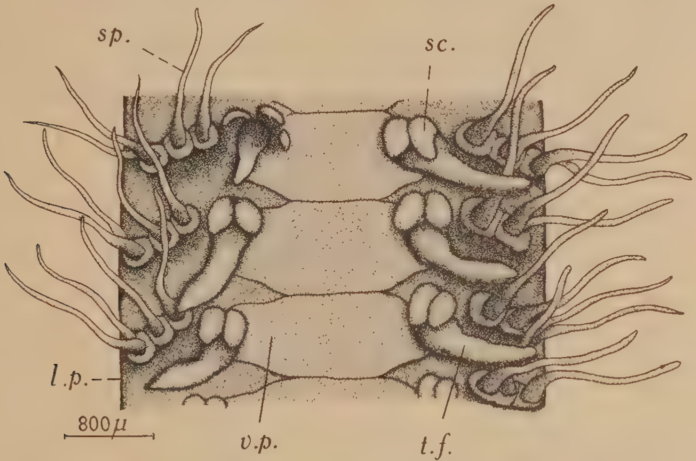


Fig. 3. A part of the oral surface of an arm of *Ophiocomina nigra*. *l.p.*, lateral arm plate; *sc.*, tentacle scale; *sp.*, arm spine; *t.f.*, tube foot; *v.p.*, ventral arm plate.

Ophiura texturata Lamarck.

In shape the tube feet of this species (Figs. 4, 5 *c*) are of an intermediate type between those of *Ophiothrix* and *Ophiocomina*. The distal end of the foot is neither drawn out into a point nor does it constitute anything akin to a sucker. The diagrammatic figure of a longitudinal section through an *Ophiura* tube foot (Fig. 5 *c*) is of a contracted fixed specimen. In life, the papillary areas are not well marked although the glands (*g*.), similar to those already described, are restricted in distribution to the rather ill-defined elevations of the ectoderm. These glandular elements are fewer in number than in *Ophiothrix* or *Ophiocomina*. The tentacle scales (Fig. 4, *sc*.) which cover the base of the tube feet are large and numerous, and the podia, which are directed towards the tip of the arm while at rest, are not capable of the same degree of extension as are the tube feet of the other two ophiuroids.

THE TUBE FEET OF ASTEROIDS, ECHINOIDS AND HOLOTHURIANS

(Marthasterias glacialis (L.), Echinus esculentus L., and Cucumaria lactea (Forbes).)

These three classes of the Echinodermata all contain members which have tube feet provided with well-developed suckers. Where the tube feet or suckers are absent the condition is undoubtedly a secondary one. Examination of the

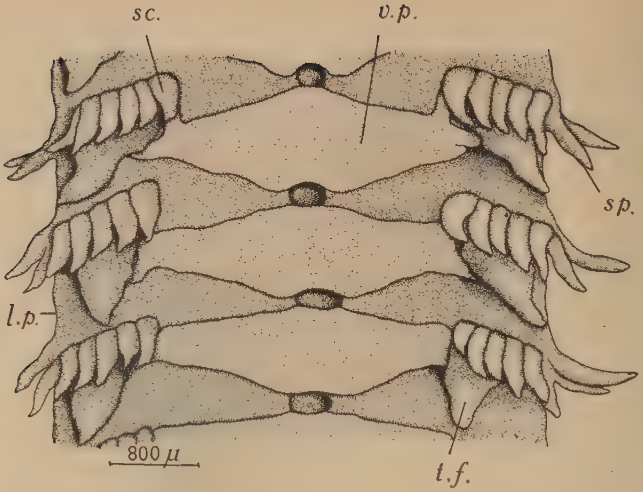

sc.
v.p.
sp.
l.p.
800 μ
t.f.

Fig. 4. A part of the oral surface of an arm of *Ophiura texturata*. *l.p.*, lateral arm plate; *sc.*, tentacle scale; *sp.*, arm spine; *t.f.*, tube foot; *v.p.*, ventral arm plate.

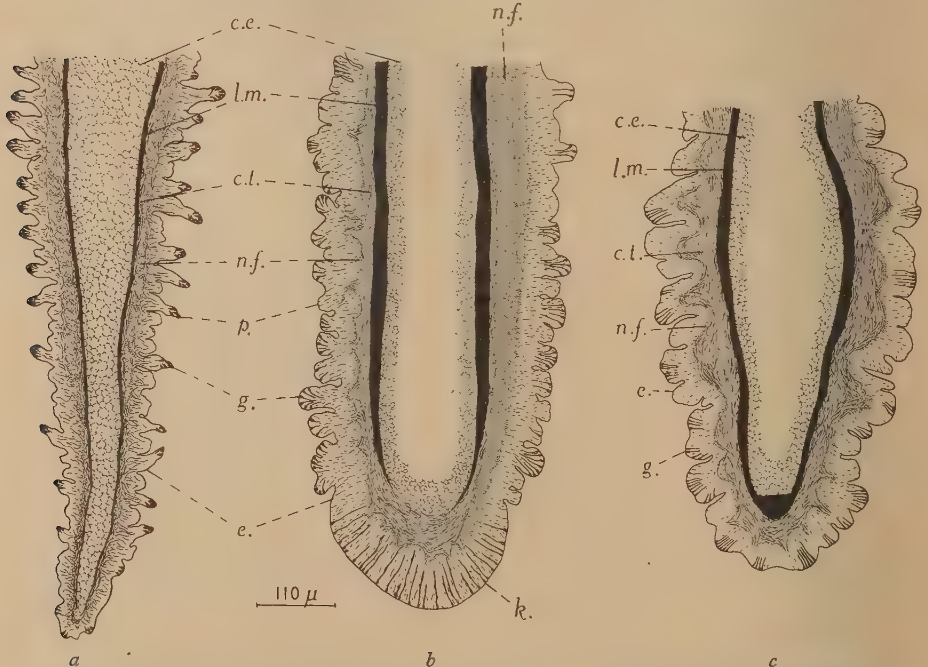

c.e.
n.f.
l.m.
c.t.
n.f.
p.
g.
e.
110 μ
k.
c.e.
l.m.
c.t.
n.f.
e.
g.
a
b
c

Fig. 5. Diagrammatic longitudinal sections of tube feet of *a*, *Ophiothrix fragilis*, *b*, *Ophiocomina nigra* and *c*, *Ophiura texturata*; the cuticle is omitted. *c.e.*, coelomic epithelium; *c.t.*, connective tissue; *e.*, epithelium; *g.*, gland; *k.*, terminal knob of the tube foot; *l.m.*, longitudinal musculature; *n.f.*, neurofibrillar plexus; *p.*, papilla.

feet of three typical members, namely, *Echinus esculentus*, *Marthasterias glacialis* and *Cucumaria lactea*, reveals an essential similarity of form of the sucker throughout the three classes. The type may be exemplified by consideration of an ambulacral tube foot of *Echinus esculentus*. The arrangement of the tissues in an *Echinus* podium is shown in Fig. 6. The outer part of the wall is constituted by a thick epidermis made up, for the most part, of ciliated epithelial cells (*e.*) covered by a thin cuticle but containing, in addition, sensory elements and, in the sucker only, glandular cells (*g.*) to which reference will later be made. Underlying the epithelium is a plexus of nerve fibrils (*n.f.*) which, at the base of the sucker, forms a nerve ring (*n.r.*). The connective tissue (*c.t.'*) consists of coarse wavy strands of tissue and is sharply demarcated into two layers, the inner being the more dense. Internal to the connective tissue are the longitudinal muscle fibres (*l.m.*) and the cells of the coelomic epithelium (*c.e.*), the latter bordering the cavity of the foot. The tube feet of *Echinus* contain spicules which are lodged in the connective tissue layer and which, in the basal plate of connective tissue, form a calcareous plate.

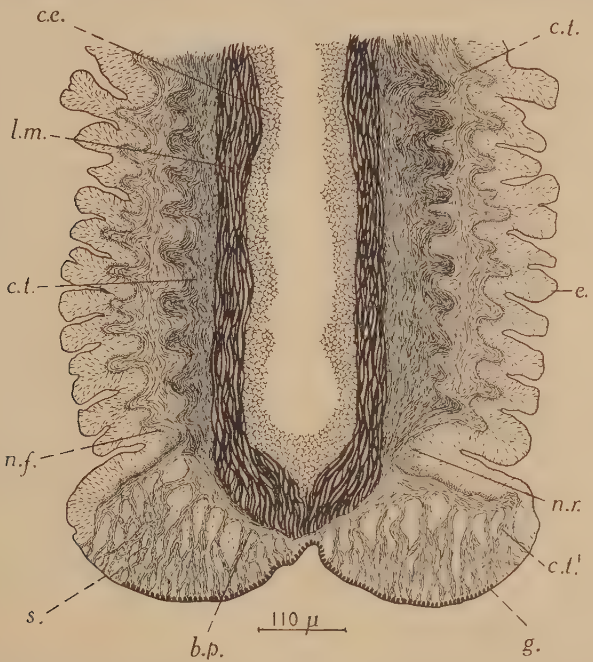


Fig. 6. A diagrammatic longitudinal section through the distal part of a tube foot of *Echinus esculentus*—the cuticle is omitted. *b.p.*, basal plate of connective tissue; *c.e.*, coelomic epithelium; *c.t.*, connective tissue; *c.t.'*, arborescent system of connective tissue fibres in the disk; *e.*, epithelium; *g.*, elongate gland of the sucker; *l.m.*, longitudinal musculature; *n.f.*, neurofibrillar plexus; *n.r.*, nerve ring; *s.*, sucker.

The sucker itself is of a complex structure. From the distal surface of the basal plate there radiate numerous arborescent connective tissue septa. The branches of the septa (Fig. 6, *c.t.'*) become finer and finer the nearer they approach the surface of the ectoderm, so that the epithelium is penetrated by a number of fine connective tissue strands all of which have their origin in the basal plate (*b.p.*). Epithelial and glandular elements are intruded between the strands. The glandular cells (*g.*) are confined absolutely to the contact surface of the sucker, and in this region, as Fig. 6 shows, they displace the epithelial cell entirely. The epithelial and glandular cells which are similar in form are long and narrow, not exceeding 5μ in width but attaining a length of 50μ or more. After fixation with Heidenhain's "Susa" mixture the cytoplasm of the cell has a finely granular appearance. The rounded or oval vesicular nucleus (Fig. 7, *n.g.*), of about 2·5μ diameter, is usually centrally placed but may be found towards the proximal or distal end of the cell. The glandular elements differ from the epithelial cells in their ability to secrete a fluid which stains readily with acid fuchsin and muchaematein and to a lesser extent with Heidenhain's iron-alum haematoxylin, Delafield's haematoxylin and Mayer's

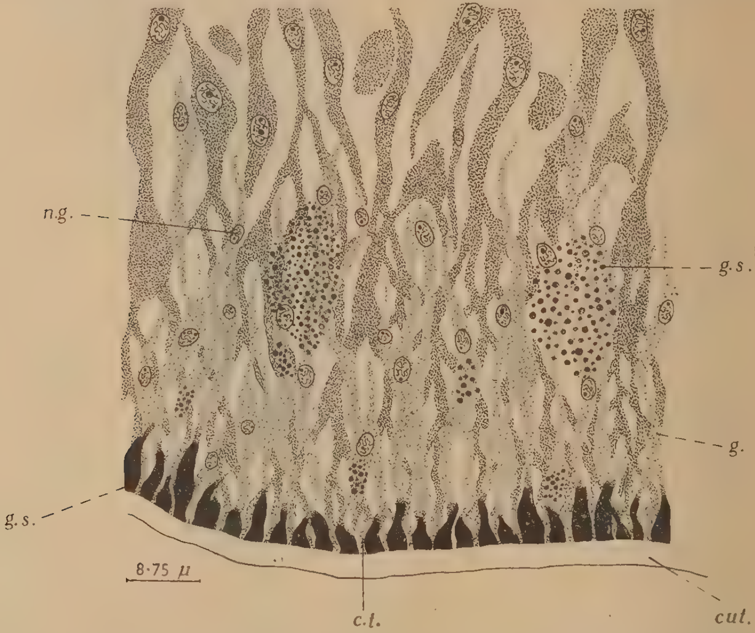


Fig. 7. A part of the wall of the tube foot sucker of *Echinus esculentus*. *c.t.*, connective tissue fibre; *cut.*, cuticle; *g.*, elongate gland of the sucker; *g.s.*, glandular secretion in distal part of gland; *g.s.'*, glandular secretion in proximal part of gland; *n.g.*, nucleus of glandular element.

mucicarmine. Each cell has a deeply staining distal portion (Fig. 7, *g.s.*) in which the secretion consists either of numerous closely apposed droplets or of a homogeneous fluid mass formed, presumably, by the flowing together of the originally separate droplets. The greater part of the gland is devoid of secretion, but, here and there, larger masses of droplets, representative of secretory activity in adjacent cells, are to be found (Fig. 7, *g.s.′*).

The tube-foot sucker of *Marthasterias glacialis* is very similar in form to that of *Echinus*. There is the same arrangement of the arborescent connective tissue and of the glandular elements; these latter are of the "Körnchendrüsenzell" type, rather longer and wider than those of *Echinus*, but occupying a similar position on the contact surface of the sucker. In *Marthasterias* it is noticeable that the glands are not confined to the sucker but are also found throughout the remainder of the tube-foot ectoderm. In this latter position, however, they are smaller, more rounded, and resemble the glands which have been described as occurring in the radial nerve cord and elsewhere (Smith, 1937).

Material for the study of the holothurian tube foot has been rather limited, and it has not been possible to determine the form of the glandular elements with any degree of certainty. It is clear, however, from the few sections of *Cucumaria* available that the deeply staining portions of the gland are terminal in position and are, as in the asteroid and echinoid, restricted to the contact surface of the tube foot. Here, as in the two latter groups, the connective tissue, with its origin in the basal plate, penetrates the ectoderm of the sucker, the finer branches terminating at the surface of the epithelium under the cuticle.

Adhesion and Locomotion in Asteroids, Echinoids and Holothurians

Reference has been made earlier in this paper to the observations of Paine (1926) on the adhesion of the tube feet of the starfish *Asterias vulgaris*. This author concluded that the average adhesive force of a single podium was approximately 18 g. per mm.^{2} of contact surface and that of this, approximately 56 % was due to suction, the remainder being due to some other factor, probably stickiness.

When a starfish applies a tube-foot sucker to the substratum, complete contact with the latter is effected by an inflow of fluid from the ampulla into the cavity of the podium. The basal plate is then pulled backward, a vacuum remaining between the central part of the disk and the surface of contact. The backward pull is effected by contraction of the longitudinal musculature, and the pull is in some way transmitted to the epithelial surface of the sucker. One cannot but conclude that the system of radiating connective tissue fibres, which is of such constant occurrence in the suckers of the tube feet of asteroids, echinoids and holothurians, is an adaptation for the transmission of the backward pull to all parts of the disk and serves for the rapid and effective establishment of the vacuum responsible for suction. This view is supported by the fact that in the ophiuroids, where there is no marked adherence by suction, the system of arborescent connective tissue fibres is lacking.

The other constant feature of the tube-foot sucker, within the three groups under consideration, is the restriction of the elongate glandular elements to the contact surface. Locomotion in an asteroid, echinoid or holothurian demands the repeated application of the sucker to the substratum, and with each application a small quantity of mucus is required to be secreted in order to provide the stickiness which reinforces the action of suction. Paine (1926) found that it was impossible to exhaust this secretion either by repeated application of the tube foot to the substratum or by treatment with chemicals. In explanation of this condition the extreme length of the glands in the region of the sucker is a factor which ought not to be ignored, for it is obvious that these glands have a mucus content much greater than that of the much smaller, more globular, glands of the rest of the ectoderm. In short we find, in the sucker of asteroid, echinoid or holothurian podia, a perfect mechanism for the exploitation of suction and of adhesion by secretion of mucus, both of which, as Paine has shown, are of almost equal importance in the attachment of the foot. For the effective production of the vacuum necessary for suction there is the longitudinal musculature acting through the connective tissue fibres, and for continuous mucus secretion there are mucus glands so constructed as to supply secretion over a long period.

Adhesion and Locomotion in Ophiuroids

Movement of an ophiuroid over a horizontal surface is effected, primarily, by sinuous movements of the arms. When the animal is advancing in a given direction it does so either with one arm directed along the line of advance or with an interradius leading. In the former case the arms adjacent to the leading one, by flexing, move the animal in a series of jerks, while in the latter instance the two pairs of arms on either side of the leading interradius are responsible for progression. It would appear, from a cursory examination, that the tube feet play no part in the progressive movement, and this was the view held by earlier workers such as Preyer (1886–7) and Hamann (1901). Brooks and Grave (1899), however, showed that in *Ophiura brevispina* the tube feet adapt themselves to irregularities of the surface and form the points on which the arms are drawn. Östergren (1904), Cowles (1910) and May (1925) corroborate this statement, and May further shows that in *Ophionereis reticulata* the tube feet are able to attach themselves to the substratum even when the latter is perfectly smooth. The tube feet are in complete extension along the length of the arm, the weight of which is thrown on a particular set of podia. The distal part of each affected foot bends at right angles to the rest of the podium and so forms a small pad on which the arm is levered forward.

Östergren's (1904) observations on *Ophiocomina nigra* indicate that this animal adopts a similar method of progression although no crooking of the podium is to be noted.

I have been able to study the movement of *Ophiocomina* in aquaria and in large glass dishes where the tube feet could be observed during the traverse of either a horizontal or of a vertical surface. Active specimens of *Ophiocomina* use, not one, but two methods of progression. The first is the quick movement dependent on flexure of the arms, such as Östergren described, and which is effected by the tube feet acting as a fulcrum on which the arm is pivoted, but the second method is strikingly similar to that adopted by an asteroid, and appears to be used chiefly in the climbing of vertical surfaces.

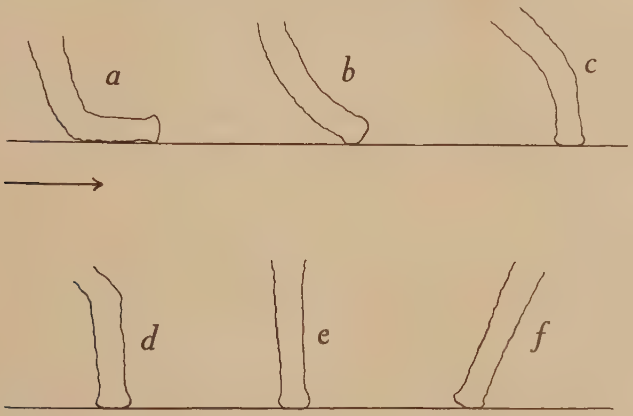


Fig. 8. The successive phases of movement (*a–f*) of the tube foot of *Ophiocomina nigra* in the climbing of a vertical surface.

When the animal starts to climb a vertical surface it pushes itself up by the disk and by the arms remaining on the horizontal substratum, the vertical progression being assisted by the movement, both by flexing and gliding, of the arms already established on the vertical surface. Once the animal has left the horizontal surface, however, the movement is entirely of a gliding nature for which the podia, alone, are responsible. The arms remain perfectly rigid, while the tube feet of all the arms move actively in a plane corresponding to the line of advance of the animal. In so doing the podia pass through the successive phases of movement indicated in Fig. 8, though not all the tube feet are in the same phase at the same moment. The tube foot stretches forward and applies the side of the sucker and the distal third of the side of the podium to the surface of the glass (Fig. 8 *a*). The terminal knob then turns so that only its tip adheres to the glass, the distal part of the podium becoming bent at an angle to the rest of the foot (Fig. 8 *c*). The foot now straightens out in the manner indicated (Fig. 8 *d*) until it is entirely vertical (Fig. 8 *e*). While the foot remains in this taut condition the animal moves forward slightly and comes to lean back at an angle to the surface (Fig. 8*f*). At this point the knob is detached with a jerk—itself indicative of former attachment—and the tube foot is stretched forward again for a re-application to the surface of the glass. If the animal be disturbed in its climb, all the feet detach themselves simultaneously and the animal falls to the bottom of the dish soon, however, to recommence its upward climb.

Although specimens of *Ophiothrix* have been kept in glass dishes for several hours at a time they have not been induced to climb up the sides of the vessels. It may be that the tube feet are unable to hold fast to such a smooth surface, for in aquaria the animals maintain themselves on the vertical walls by bending their arms round the irregularities of the surface or by pressing themselves into the corners of the tank. *Ophiothrix* will hold themselves on to a vertical wall merely by the attachment of their podia, but the adhesive process is not so effective as in *Ophiocomina*. Adhesion is here effected by the application of the greater part of the sides of the tube feet to the substratum, the podia being held at right angles to the long axis of the arm, in which position the papillae, with the mucus glands at their tips, are able to maintain contact.

Conclusion and Summary

Comparison of the methods of adhesion and locomotion of the typical members of the four classes of the Eleutherozoa reveals a similarity of the adhesive mechanism in the Asteroidea, Echinoidea and Holothuroidea in that adhesion is due in part to suction and in part to the secretion of mucus. The ophiuroid, on the other hand, has tube feet which, because of their lack of a well-defined sucker, must adhere merely by their intrinsic stickiness. The ability to make use of suction results from the possession of a sucker so fashioned that the median part of the disk may be withdrawn from the surface of contact, with the resultant production of a vacuum. The sucker of the asteroid, echinoid or holothurian tube foot is well adapted for this purpose. An essential feature of such a disk is the presence of an arborescent system of connective tissue fibres extending from the basal plate to the outer limit of the ectoderm. By means of this system, the pull initiated by contraction of the longitudinal musculature of the podium is transmitted to the ectoderm of the sucking disk, the central part of which is thereby lifted up. Where suction plays no part in adhesion, as in the Ophiuroidea, the arborescent system of fibres is lacking.

The ability to secrete mucus is an important subsidiary factor in the adhesion of the asteroid podium and may probably be of equal importance in the echinoid and holothurian, although the method of attachment in these latter two groups has not been analysed. Locomotion demands continued re-application of the tube-foot disk to the substratum; accordingly, we find, in the three classes mentioned, that especially elongate mucus glands are present and that these are confined to the adhesive surface of the sucker. In *Ophiothrix* and probably most of the ophiuroids, however, it is the side of the tube foot which is pressed against the substratum; in this instance the mucus glands are distributed over the sides of the podium and are confined to the surfaces of contact, namely, the papillae.

Finally, it may be noted that *Ophiocomina nigra* resembles, in some degree, the asteroid, echinoid and holothurian in that its tube feet are furnished with rudimentary suckers. The terminal knob is well provided with glandular elements, and, although it may not adhere by suction, its sticky secretion enables the animal to perform walking movements and to maintain its position both on horizontal and on vertical surfaces.

REFERENCES

Brooks, W. K. and Grave, C., 1899. *Ophiura brevispina. Mem. Nat. Acad. Sci· Washington*, Vol. 8, 4th memoir, pp. 79–100.

Cowles, R. P., 1910. Stimuli produced by light and by contact with solid walls as factors in the behaviour of Ophiuroids. *Journ. Exp. Zool.*, Vol. 9, No. 2, pp. 386–416.

Hamann, O., 1889. Die Anatomie und Histologie der Ophiuren und Crinoiden. *Beiträge zur Histologie der Echinodermen*. Jena.

Hamann, O., 1901. *Bronn's Klassen und Ordnungen des Thier-reichs*. Bd. 2, Abt. 3.

May, R. M., 1925. Les réactions sensorielles d'une Ophiure (*Ophionereis reticulata*). *Bull. Biol. France et Belge*, T. 50, pp. 372–402.

Östergren, H., 1904. Über die Funktion der Füsschen bei der Schlangensternen. *Biol. Centralbl.*, Bd. 24, pp. 559–65.

Paine, V. L., 1926. Adhesion of the tube feet in starfishes. *Journ. Exp. Zool.*, Vol. 45, pp. 361–6.

Preyer, W., 1886–7. Über die Bewegungen der Seesterne. *Mitt. Zool. Stat. Neapel.*, Bd. 7, pp. 27–127.

Smith, J. E., 1937. On the nervous system of the starfish *Marthasterias glacialis* (L.). *Phil. Trans. Roy. Soc.*, Ser. B, Vol. 227, pp. 111–73.

RELATION OF BACTERIA TO DIATOMS IN SEA WATER*

By Selman A. Waksman, J. L. Stokes
and Margaret R. Butler
Woods Hole Oceanographic Institution

The functions of the two major constituent groups of the phytoplankton, namely, the diatoms and the bacteria, are supplementary to one another in the cycle of life in the sea: the diatoms synthesize organic matter from the simple chemical substances produced in the decomposition or mineralization of organic matter in the sea by the bacteria. Although the general aspects of the activities of these two groups of organisms are fairly well known, their mutual interrelationships still remain to be determined. The following studies were carried out in an attempt to elucidate this important problem.

METHODS

Four methods were used in these investigations: (1) Oxygen consumption in sea water enriched with diatom material; the oxygen being determined by a modification of the Winkler method. (2) Nitrogen transformation in the water, as a result of bacterial activities; the nitrogen being determined either directly as ammonia or indirectly, namely by an increase in oxygen consumption as a result of addition of glucose to the water; it had been previously found (Waksman & Carey, 1935) that the rate of glucose decomposition in sea water is controlled by the available nitrogen in the water. (3) Regeneration of the phosphorus, the latter being determined by the Atkins-Denigès method. (4) Increase in bacterial numbers, as measured by the plate method.

In most of the previous experiments on decomposition of organic matter in sea water (Waksman, Carey & Reuszer, 1933), excessive amounts of plankton material were added to the water. This resulted in appreciable changes in the aqueous medium, particularly the rapid consumption of the oxygen, whereby the system became changed from a purely aerobic to a distinctly anaerobic one. In the following experiments, mixed and pure plankton were added in concentrations not greatly in excess of those frequently found in natural sea water. Studies were also made of the transformation of marine plankton in the same vessel in which it had been synthesized.

---

* Contribution No. 157 of the Woods Hole Oceanographic Institution and Journal Series Paper, Department of Soil Microbiology, N.J. Agricultural Experiment Station.

Decomposition of Dead Diatom Material by Bacteria

Two samples of diatom plankton consisting almost entirely of *Rhizosolenia* were collected in Vineyard Sound at Woods Hole. Analysed, on a dry basis, they gave 10·46 and 7·34 % carbon, and 1·52 and 1·05 % nitrogen, giving respective C : N ratios of 6·9 and 7·0; the phosphorus content of the mixed diatom material was 0·41 %, calculated as PO_4. These samples were mixed carefully and used in some of the following experiments.

Five and ten mg. portions of this plankton, in an air-dry state, were placed in standard glass-stoppered oxygen bottles of approximately 220 c.c. capacity. The bottles were filled either with fresh, filtered sea water or with the same sea water enriched with 10 mg. of glucose per litre. The bottles were then incubated in the dark under water at a temperature of 20–22° C. The process of decomposition was followed by removing some of the bottles at different time intervals and analysing them for their oxygen, phosphate and bacterial content.

The results reported in Table I are typical of those obtained in several other experiments. In the sea water alone, the familiar sequence of a rapid bacterial multiplication, which in this instance reached a peak within 2 days, followed by a sharp drop to a low and fairly constant level, occurred (Waksman & Carey, 1935; Waksman & Renn, 1936; Renn, 1937). Oxygen consumption was parallel with the increase in bacteria. Phosphate was also consumed during the logarithmic growth phase of bacterial multiplication; the lowest phosphate values coincided with the highest bacterial counts. However, as the bacterial cells began to die off and autolyse, phosphate was rapidly regenerated in the water. The increase of 20 mg. of PO_4 per $m.^3$ of sea water, at the end of 420 hr. of incubation, over the amount originally present, represents the phosphate liberated from the organic matter originally present in the sea water, either in true solution or suspension, and susceptible to bacterial attack.

In the water to which diatom material had been added, somewhat different results were obtained. Since the dead diatoms were an available food supply for the bacteria present in the water, a higher bacterial count was obtained than in the sea water alone. With 5 mg. of diatom material present, the maximum count of 1,440,000 bacteria per 1 c.c. was obtained in 36 hr. With 10 mg. of diatom material present, the maximum number of bacteria was 2,000,000 per 1 c.c. in 12 hr. This indicates that the dead diatom material was quickly attacked and decomposed by the bacteria. The phosphate content of the sea water increased continuously throughout the duration of the experiment. Although some phosphate was no doubt utilized by the bacteria in the synthesis of their cell substance, there was more phosphate liberated from the diatom material by the bacteria than they could themselves assimilate. There resulted, therefore, a gradual increase in the PO_4 content of the sea water. This inability of the bacteria to utilize all the phosphate that they had liberated was due to an insufficient supply of available energy which limited bacterial multiplication, as will be shown later. At the end of 420 hr. the minimum increase in phosphate content of the sea water was 66 mg. per $m.^3$, due to the decomposition of 5 mg. of the diatom material per bottle and to autolysis of the subsequently synthesized bacterial substance. When 10 mg. of this material was used the phosphate increase was 111 mg. per $m.^3$ The amounts of phosphorus added in the diatom material were equivalent to 92·5 and 185 mg. PO_4 per $m.^3$ respectively. It can thus be seen that approximately two-thirds of the total PO_4 present in the diatom material was liberated into the sea water as a result of bacterial activities, within 420 hr. and usually within 132 hr.

It is interesting to compare these results with those obtained by Cooper (1935), who found soluble phosphate to be liberated rapidly in the decomposition of plankton material, but less rapidly with diatom material than with animal plankton.

When an additional energy supply was added to the sea water, in the form of glucose, a marked increase in oxygen consumption, phosphate utilization and bacterial multiplication took place in sea water with and without the addition of 5 mg. of diatom material. The phosphate content of the water in both cases dropped within 12 hr. to less than 30 mg. per $m.^3$, which is the lower limit of the analytical method. Regeneration of the phosphate did not occur until after 96 hr. of incubation when the bacterial numbers had been greatly reduced. That available nitrogen was liberated in the decomposition of the diatom material is best shown by the high bacterial count of 7,000,000 per 1 c.c. in the presence of glucose.

Since all or practically all of the PO_4 had been removed from the water in a very short time, in the presence of glucose, it was thought that it might be of interest to determine whether the lack of a sufficient supply of available PO_4 was a limiting factor in the decomposition of the diatom material by the bacteria. In the following experiment an excess of PO_4 was added to the sea water, and only 5 mg. portions of the diatom material were used. The results are reported in Table II. In the sea water alone and in the presence of diatom material, a consumption of 188 mg. PO_4 per $m.^3$ occurred within 60 hr. Within the same period of time, the sea water to which 10 mg. of glucose had been added showed a loss of 348 mg. of PO_4 per $m.^3$, whereas the sea water containing both diatom material and glucose showed a loss of 368 mg. PO_4 per $m.^3$ After 60 hr. a gradual regeneration of the phosphate took place. The greatly increased rate of oxygen absorption and phosphate utilization seems to indicate that the diatoms decomposed more rapidly in the presence of an excess of phosphate.

The results of these two typical experiments are thus sufficient to demonstrate clearly that dead diatoms can serve as a readily available food supply for bacteria, the diatoms being rapidly decomposed and the nitrogen and phosphorus rapidly liberated in available forms.

TABLE I. DECOMPOSITION OF DEAD DIATOM MATERIAL IN SEA WATER BY BACTERIA

	Sea water alone			Diatom material 5 mg.			Diatom material 10 mg.			Glucose 10 mg.			Glucose 10 mg. + diatom material 5 mg.		
Incubation hours	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.
0	0	126	10,400	0	126	10,400	0	126	10,400	0	126	10,400	0	126	10,400
12	0·04	131	690,000	0·50	135	1,410,000	0·78	147	2,000,000	0·62	< 30	470,000	1·02	< 30	2,200,000
24	0·15	128	770,000	0·67	143	900,000	1·35	149	1,290,000	2·66	< 30	2,180,000	3·40	< 30	7,600,000
36	0·19	98	850,000	0·90	149	1,440,000	1·41	-	1,310,000	3·69	< 30	2,170,000	4·32	< 30	5,200,000
48	0·33	—	—	1·02	—	—	1·72	—	—	3·98	—	—	4·66	—	—
60	0·38	135	600,000	1·05	148	1,150,000	1·96	173	750,000	4·20	< 30	730,000	4·97	< 30	1,860,000
96	0·50	—	—	1·59	171	61,000	2·56	192	142,000	5·69	64	35,000	5·74	82	260,000
132	0·78	144	6,100	1·92	209	—	2·66	244	109,000	5·80*	118	—	—	165	124,000
252	—	—	3,100	2·26	—	28,000	3·83	—	60,000	—	149	1,500	—	—	100,000
420	1·72	146	1,800	2·60	212	12,700	4·66	257	24,000	—	—	2,100	—	—	17,800

* Oxygen used up completely.

TABLE II. INFLUENCE OF AVAILABLE PHOSPHORUS UPON DECOMPOSITION OF DEAD DIATOM MATERIAL

	Sea water alone			Diatom material 5 mg.			Glucose 10 mg.			Glucose 10 mg. + diatom material 5 mg.		
Incubation hours	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO$_4$ γ/l.	Bacteria in 1 c.c.
0	0	1,404	550	0	1,404	550	0	1,404	550	0	1,404	550
16	0·37	1,388	42,000	0·53	1,384	730,000	0·37	1,400	86,000	0·70	1,400	620,000
24	0·65	—	77,000	1·02	—	550,000	1·16	1,328	590,000	2·30	1,304	5,300,000
36	0·82	1,392	110,000	1·28	1,340	1,460,000	3·04	1,248	1,110,000	3·73	1,192	5,700,000
48	0·93	—	199,000	1·56	1,224	690,000	3·78	1,180	1,710,000	4·47	—	5,800,000
60	1·02	1,216	147,000	1·74	1,216	630,000	4·24	1,056	1,690,000	5·15	1,036	6,000,000
108	1·38	1,316	41,000	2·33	1,376	—	5·38*	1,128	640,000	—	1,288	1,000,000
264	2·02	1,448	9,800	3·33	1,392	42,000	—	1,336	174,000	—	1,448	188,000

* Oxygen used up completely

RELATIONSHIP OF BACTERIA TO LIVING DIATOMS

In these investigations diatom cultures containing bacteria, bacteria-free diatom cultures and freshly collected mixed diatom plankton were used.

A culture of *Nitzschia closterium* originally obtained from Dr E. J. Allen, of the Plymouth Laboratory, was grown on the standard nutrient Miquel-Allen medium, in 500 c.c. Erlenmeyer flasks, for a period of 20–30 days. The contents of several flasks were combined, centrifuged and washed with fresh sea water, again centrifuged and the residue suspended in sea water. Varying amounts of the diatom suspension were added to 220 c.c. oxygen bottles containing fresh sea water. The bottles were incubated in the dark, at room temperature under water, and analysed at various intervals. The bacterial content of 1 c.c. of the concentrated *Nitzschia* material was 4,800,000 and the diatom content 18,400,000; the fresh sea water contained 12,000 bacteria in 1 c.c. The results presented in Table III show that the *Nitzschia* cells added to fresh sea water underwent a certain amount of oxidation; this was accompanied by the liberation of phosphate, but not by an appreciable increase in bacterial numbers. The increased consumption of the oxygen may have been due partly to the respiration of the diatoms and partly to bacterial decomposition. Maximum bacterial multiplication and phosphate liberation were obtained after 8 days, with the highest concentration of the *Nitzschia* cells. At this stage, practically all the phosphate present in the *Nitzschia* material had been regenerated, as is easily calculated from the N/PO_4 ratio of 7/3; this ratio was found for the mixed diatom plankton. Dr H. W. Harvey‡ has suggested that it is quite possible for some of the phosphate to be introduced as precipitated ferric phosphate with the *Nitzschia* culture, which would account in part for the high phosphate recovery.

TABLE III. RELATION OF BACTERIA TO ENRICHED CULTURE OF *NITZSCHIA CLOSTERIUM* ADDED TO SEA WATER

Nitzschia culture added per litre* c.c.	Oxygen consumed c.c. per litre				Bacteria in 1 c.c.			Phosphate γ per litre	
	1 day	3 days	6 days	8 days	1 day	3 days	8 days	6 days	8 days
0	0·48	0·69	0·90	—	850,000	750,000	30,000	70	—
2·3	0·66	2·19	2·79	3·39	690,000	575,000	46,000	110	210
4·5	0·81	2·52	5·16	5·22†	800,000	2,750,000	76,000	420	380
9·0	1·05	2·34	5·22†	5·22†	650,000	405,000	825,000	300	680

* The dry matter content in the *Nitzschia* suspension was calculated from the total nitrogen (0·14 mg. per 1 c.c.) to be equivalent to 1 mg. organic carbon in 1 c.c.

† Oxygen used up completely.

This experiment was repeated, using younger (12-day-old) cultures of the diatom material and concentrating it by centrifuging, to give a preparation which contained 9,200,000 *Nitzschia* and 3,100,000 bacteria per 1 c.c. The results of this experiment (Table IV) confirmed the previous observation that, in the presence of a living culture of *Nitzschia*, the bacterial activities were very limited. No nitrogen was liberated, as shown by the fact that the addition of glucose to the cultures brought about no increase in oxygen consumption: with 2·3 c.c. *Nitzschia* suspension added per litre of water, the increase in oxygen consumption was, without glucose, 0·87 c.c. and with glucose 0·72 c.c.; with 4·5 c.c. of the diatom culture, the corresponding increases were 2·10 and 1·29 c.c. respectively. The addition of nitrate to the water did not stimulate to any great extent the destruction of the diatoms.

---

‡ Personal communication.

In order to eliminate the interfering factor which might have resulted from the introduction into the fresh sea water of large numbers of bacteria, and also for the purpose of determining the consumption of oxygen as a result of diatom respiration, bacteria-free cultures of the diatom were used.

Table IV. Influence of Nitrogen and Glucose on the Oxidation of *Nitzschia closterium*

Nitzschia culture added per litre c.c.	Nitrate nitrogen added per litre mg.	Glucose added per litre mg.	Oxygen consumed c.c. per litre			Nitrate N mg. per litre		Bacteria in 1 c.c.
			2 days	6 days	10 days	2 days	6 days	6 days
0	0	0	0·39	0·63	0·78	0·01	0·01	12,000
2·3	0	0	0·63	1·20	1·65	0·01	0·01	18,000
4·5	0	0	0·81	1·56	2·88	0·01	0·01	19,000
9·0	0	0	1·05	3·45	5·16*	0·01	Trace	450,000
0	0·07	0	0·45	0·69	0·69	0·10	0·10	—
4·5	0·07	0	0·93	2·01	2·85	0·01	Trace	—
9·0	0·07	0	1·47	3·81	4·62	0·01	Trace	—
0	0	5	0·63	1·62	2·52	—	—	55,000
2·3	0	5	0·69	2·16	3·24	—	—	70,000
4·5	0	5	0·63	2·34	3·81	—	—	330,000

* Oxygen used up completely.

A culture of *Nitzschia closterium* was obtained from Dr C. B. van Niel. It was grown for 13 days in Miquel solution, centrifuged and washed with fresh sterile sea water under sterile conditions and resuspended in sterile sea water. There were 8,500,000 diatom cells in 1 c.c. of suspension. One-half and 2 c.c. portions of this suspension were placed in oxygen bottles and filled with paper filtered sea water, previously kept overnight in the laboratory. In order to determine the oxygen consumption due to the respiration of the diatoms, controls containing the same amounts of diatom suspension were placed in sterile oxygen bottles, and filled with sea water which had been previously sterilized by heating at 15 lb. pressure for 20 min. The oxygen content of the sterile sea water was less than that of the fresh sea water due to the difficulty encountered in resaturating the water with oxygen after sterilization. All the bottles were placed in the dark under water and analyses made at different intervals. The results given in Table V show that during the first 88 hr. of incubation the excess oxygen consumption in the sea water containing 2 c.c. diatom suspension over the oxygen consumption in the sea water alone can be accounted for by the respiration of the diatoms, since the sea water plus 2 c.c. diatom suspension consumed 1·81 c.c. oxygen per litre and the sea water alone 1·53 c.c. per litre, while the consumption of oxygen in the sterilized sea water plus 2 c.c. diatom suspension was 0·35 c.c. per litre. By adding the latter two figures, a consumption of 1·88 c.c. oxygen per litre is obtained; this is very close to the 1·81 c.c. oxygen consumed in the fresh sea water to which the diatom suspension had been added.

A microscopic examination of the centrifuged sediment at this point revealed that the diatoms were in all cases in good physical condition (chromatophores intact). It may therefore be concluded that living diatoms are not attacked by the bacteria. However, the bacterial counts showed that a greater development of bacteria took place in the presence of the diatoms than in their absence. This confirms the previous observations of Gran (1933) that there is a certain parallelism between the development of diatoms and bacteria in sea water.

TABLE V. RELATIONSHIP BETWEEN PURE CULTURES OF LIVING DIATOMS AND BACTERIA

	Fresh sea water		Fresh sea water +0·5 c.c. diatom culture		Fresh sea water +2 c.c. diatom culture		Sterile sea water+ 0·5 c.c. diatom culture	Sterile sea water+ 2 c.c. diatom culture
Incubation hours	Oxygen consumed c.c./l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	Bacteria in 1 c.c.	Oxygen consumed c.c. l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	Oxygen consumed c.c. l.
0	0	400	0	400	0	400	0	0
20	0·34	1,000	0·40	185,000	0·74	10,000	0·06	—
42	0·80	39,000	0·80	133,000	1·03	312,000	0·14	0·34
88	1·53	—	1·55	—	1·81	—	0·17	0·35
136	1·84	74,000	2·18	81,000	2·74	98,000	0·23*	0·46*
184	2·10	77,000	2·42	158,000	2·96	107,000	0·46*	0·55*
256	—	—	—	—	—	—	1·03*	1·03*
20 days	2·33	900	2·99	3,700	3·69	9,200	—	—

* Water became contaminated with bacteria.

After 136 hr. incubation, an examination of the centrifuged sediment showed that the diatoms in the unsterilized sea water were badly disintegrated. The chromatophores were completely gone in many cases, and the cells were difficult to see because of changes in refractive index due to death. A number of Protozoa were found to be present in the water. The bacterial numbers showed a decreasing population, with the exception of the untreated sea water in which the peak had not yet been reached. Unfortunately, at this point, the sterile sea water to which the diatom culture had been added became contaminated with bacteria.

A comparative study was now made of the relationship of bacteria to living and dead diatoms added to fresh sea water. Two series of oxygen bottles, one with and one without 5 mg. glucose per litre, received sea water enriched with PO_4 (100 mg. per m.^{3}). Each series was divided into three sets: (1) sea water alone; (2) 2 c.c. of a concentrated suspension of living *Nitzschia* (16,000,000 diatoms per 1 c.c. of suspension); (3) the same amount of diatom material, heated at 60–62° C. for 45 min. in order to kill the diatoms.

The results presented in Table VI show that the living diatoms and not the bacteria were the agents responsible for the rapid phosphate consumption. This is definitely demonstrated by the fact that the control sea water having, after 1 day, a higher bacterial count than the sea water with the 2 c.c. of living diatoms, showed a PO_4 consumption of only 28 mg. per m.^{3}, as compared with the complete or almost complete consumption of the 298 mg. of PO_4 in the sea water with the living diatoms. This fact is even more sharply brought out in the water containing glucose. In spite of the presence of glucose, which so readily stimulates bacterial multiplication, the bacterial count in the sea water plus living diatoms remained relatively low, while the phosphate and oxygen were rapidly consumed. Living diatoms can therefore be considered as successful competitors of bacteria for the available nutrients, and may represent one of the factors which tend to limit bacterial multiplication in the sea. The process of initial phosphate utilization and subsequent regeneration is again clearly indicated. On the 5th day, a sharp increase was found in the number of bacteria in the water receiving living diatoms. A microscopic examination of the centrifuged material showed that the diatoms had disintegrated in large measure. The bacterial increase was therefore due to the decomposition of the dead diatoms.

Relationship of Bacteria to Fresh Marine Plankton

Five samples of plankton were obtained by means of a No. 20 silk net on August 3–4 1936, one at a station in Nantucket Sound (No. 1) and four at stations on George's Bank (Nos. 2–5). The plankton was washed free from sedimentary material, using fresh sea water. It was then allowed to settle and concentrated plankton thus obtained. Different amounts of the freshly collected samples of plankton were added to a series of oxygen bottles containing fresh sea water obtained from the same stations. The bottles were incubated in the dark, and analysed for oxygen, bacterial numbers and phosphate. Sample No. 1 contained 10,536 diatoms per 1 c.c., mostly *Chaetoceras*, *Skeletonema* and *Rhizosolenia*; sample No. 2, 3,159 diatoms, mostly *Rhizosolenia*; No. 3, 19,025, No. 4, 24,450, and No. 5, 16,925, mostly *Rhizosolenia* and *Nitzschia*. The plankton of the last three stations consisted almost entirely of diatoms. The carbon content of the plankton was calculated from the nitrogen content using the ratio of C : N = 7 : 1. The results presented in Table VII show that considerable oxygen consumption took place in all cases; the phosphate was liberated in a soluble form. These processes were not

TABLE VI. RELATIONSHIP BETWEEN BACTERIA, AND LIVING AND DEAD DIATOMS IN SEA WATER

100 γ PO_4 added per litre

	Sea water alone			Living diatoms*			Dead diatoms*		
Incubation days	Oxygen consumed c.c./l.	PO_4 γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO_4 γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO_4 γ/l.	Bacteria in 1 c.c.
0	0	298	400	0	298	400	0	298	400
1	0·14	270	184,000	0·40	<30	117,000	0·94	270	430,000
3	0·57	282	5,000	0·97	<30	190,000	1·20	280	20,000
5	0·62	298	20,000	1·42	185	70,000	1·93	314	18,000
7	0·80	301	5,700	1·77	319	26,000	2·11	338	11,700

5 mg. glucose and 100 γ PO_4 per litre

	Sea water alone			Living diatoms*			Dead diatoms*		
Incubation days	Oxygen consumed c.c./l.	PO_4 γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO_4 γ/l.	Bacteria in 1 c.c.	Oxygen consumed c.c./l.	PO_4 γ/l.	Bacteria in 1 c.c.
0	0	298	400	0	298	400	0	298	400
1	1·71	<30	2,080,000	0·77	<30	52,000	1·99	<30	710,000
3	2·63	170	8,000	2·05	<30	35,000	3·76	167	90,000
5	3·36	203	5,000	3·26	<30	141,000	4·39	258	51,000
7	3·53	237	11,000	3·93	94	158,000	4·79	256	8,500

* 2 c.c. of concentrated diatom culture, containing 16,000,000 *Nitzschia* cells in 1 c.c.

always accompanied by corresponding increases in bacterial numbers, especially in the diatom-rich plankton. With the exception of Station 3, there was a certain parallelism between the concentration of the plankton in the samples and the rate of oxygen consumption. The plankton of Station 1 and to some extent of Station 2 was rich in copepods, which may account for the greater abundance of bacteria in the water receiving these two samples of plankton. The most significant result of this experiment is the lack of correlation between oxygen consumption in the water receiving diatoms and bacterial multiplication.

TABLE VII. RELATION OF BACTERIA TO FRESHLY COLLECTED MIXED DIATOM PLANKTON

Station no.	Plankton added per litre c.c.*	Oxygen consumed c.c. per litre			Bacteria in 1 c.c.				Phosphate γ per litre
		1 day†	3 days	7 days	Start	1 day	3 days	7 days	7 days
1	0	0·78	—	—	20,100	1,160,000	—	28,000	30
1	4·5	0·88	1·41	1·77	32,200	2,170,000	49,000	21,000	40
1	9·0	1·14	1·53	1·89	—	2,250,000	72,000	25,500	40
1	22·5	1·18	1·77	1·98	—	2,450,000	81,000	22,000	120
2	0	0·51	—	0·83	5,800	279,000	—	46,500	40
2	4·5	0·48	0·99	1·25	7,200	307,000	75,000	72,000	60
2	9·0	0·62	1·35	1·79	—	740,000	131,000	52,500	50
2	22·5	1·29	2·97	3·77	—	2,030,000	270,000	39,000	150
3	0	0·42	—	0·99	4,200	1,050,000	—	62,000	50
3	4·5	0·61	1·03	1·65	24,000	915,000	240,000	57,500	80
3	9·0	0·65	1·71	1·74	—	990,000	375,000	59,500	90
4	0	0·39	—	0·90	12,400	940,000	—	38,500	70
4	4·5	0·75	1·38	1·98	9,500	—	355,000	65,000	80
4	9·0	0·91	2·14	3·15	—	980,000	245,000	—	—
5	0	0·31	—	0·84	2,700	550,000	—	109,000	30
5	4·5	0·54	1·71	2·88	6,600	790,000	330,000	56,000	100
5	9·0	0·57	2·75	5·01	—	1,720,000	365,000	51,000	120

* The carbon content of 1 c.c. of the five samples of plankton were as follows: No. 1, 0·05 mg.; No. 2, 0·06 mg.; No. 3, 0·37 mg.; No. 4, 0·22 mg.; No. 5, 0·23 mg.

† 42 hr. for Station 1.

RELATION OF BACTERIA TO FRESHLY SYNTHESIZED DIATOM MATERIAL

It has been shown previously (Waksman & Renn, 1936) that the processes resulting from diatom oxidation in sea water could be better elucidated, if growth of the diatoms was first permitted to take place in closed containers, and photosynthesis then stopped by placing the containers in the dark. Conditions are thus obtained which approach more nearly those found in nature. In order to increase the amount of synthesized diatom material above that normally present in sea water, an enriched medium was employed. This consisted of fresh sea water, to which 5 mg. KNO_3, 2 mg. K_2HPO_4 and 2 mg. $FeCl_3$ had been added per litre. The enriched water was distributed in glass-stoppered oxygen bottles, and these incubated at room temperature, under water and in the light, in glass aquaria. After different periods, a few of the bottles were removed. Some were analysed at once and some were transferred to a water bath kept dark at room temperature, and allowed to remain under water for 5–12 days. In those bottles, where extensive photosynthesis took place, the water became supersaturated with oxygen, some of which being liberated in a gaseous form, was lost, thus modifying the results of some of the oxygen determinations.

Gradual consumption of the oxygen took place in those bottles which were incubated in the dark (Table VIII). In the light, oxygen was rapidly liberated, due to the photosynthetic activity of the diatom population in the enriched sea water; after 7 days, the nitrate disappeared completely; the phosphate was present in excess of the requirements of the diatoms; the oxygen increased by 4·62 c.c. per litre of water. When the bottles were now placed in the dark, there was a reduction of 1·08 c.c. in the oxygen content per litre in 2 days, and of 2·64 c.c. in 11 days. When photosynthesis was allowed to proceed for 13 days, the oxygen content of the water increased by 9·39 c.c. per litre; incubation in darkness following this period resulted in a decrease of 1·02 c.c. in oxygen concentration in 5 days, and of 3·65 c.c. oxygen in 12 days. The consumption of phosphate in the light was 470 (890–420) γ per litre in 7 days, and 500 (760–260) γ in 13 days. When oxidation of the diatoms began, the phosphorus was regenerated as phosphate, but only very slowly. The gradual disappearance of the phosphate in the water kept in the dark was due either to its partial consumption or to its precipitation as insoluble phosphate, as a result of addition of iron, as ferric chloride.

TABLE VIII. SYNTHESIS AND OXIDATION OF DIATOM MATERIAL IN ENRICHED SEA WATER*

Incubation of bottles, days		On basis of 1 litre of water			
			Phosphate		
Light	Dark	Oxygen above (+) or less (−) than the control c.c.	Left γ/l.	Regenerated as a result of incubation in the dark γ/l.	Bacteria in 1 c.c.
7	—	+4·62	420	—	145,000
7	2	+3·54	500	80	72,000
7	11	+1·98	460	40	6,000
13	—	+9·39	260	—	103,000
13	5	+8·37	310	50	120,000
13	12	+5·74	330	70	35,000
—	7	−0·30	890	—	30,000
—	13	−0·42	760	—	72,000

* The nitrate nitrogen added and found in control water was 0·76 mg. per litre; it completely disappeared in the bottles incubated for 7 days in the light.

Considerable variation was found among the individual bottles in the previous experiments. This may account for some of the discrepancies obtained in certain determinations. In order to check this, the results of another experiment are reported here. In this, all the determinations were made at least in duplicate and sometimes in triplicate; the analyses were also carried out at more frequent intervals (Table IX). Only one concentration of nitrate was used, namely 5 mg. KNO_3 per litre. The maximum amount of photosynthesis, as measured by the oxygen liberated, was attained in 7 days; nitrate assimilation continued even after the maximum was attained. At that time, oxidation of the synthesized material seemed to coincide with assimilation. When photosynthesis was stopped, by incubating the bottles in the dark, rapid oxidation of the diatoms took place, especially at the 5–7 day periods when the diatom population in the water was carrying out its most active photosynthesis. The ratio between nitrogen and phosphate assimilation, for the first three days of photosynthesis, was $\frac{0{\cdot}43}{0{\cdot}15}$ or 2·9 : 1, and for the 5 day period, $\frac{0{\cdot}73}{0{\cdot}36}$ or 2·0 : 1.

TABLE IX. RELATION OF BACTERIA TO OXIDATION OF DIATOM PLANKTON

Incubation of bottles, days		Oxygen content per litre	Nitrate N per litre	Phosphate γ per litre		Bacteria
Light	Dark	c.c.	mg.	Left	Regenerated	in 1 c.c.
0	0	5·38	0·84	850	—	12,000
3	0	7·65	0·41	700	—	182,000
3	5	7·07	—	750	50	31,000
5	0	15·18	0·11	490	—	—
5	5	9·51	0·13	670	180	—
7	0	17·47	0·16	470	—	132,000
7	5	12·27	—	610	140	15,000
10	0	17·42	0·03	340	—	126,000
10	5	12·62	—	—	—	28,000
12	0	17·66	—	340	—	42,000
12	5	13·06	—	—	—	75,000

When the bacterial numbers are examined, it is found that the oxidation processes taking place in the freshly synthesized diatom cultures were not accompanied by any appreciable increase of bacteria. To be sure, there were more bacteria in the bottles in which photosynthesis took place. Nevertheless, the bacterial population, as determined by the plate method, remained comparatively limited, even with the large amounts of fresh diatom material undergoing active oxidation in the dark. Those bacteria that were found in the bottles grew very slowly on the plates and required at least 7 days' incubation for an adequate count. One must, therefore, conclude that bacteria do not play any important role in the oxidation of fresh diatom material.

A microscopic examination of the plankton, centrifuged after varying periods of photosynthesis, revealed the presence of large numbers of diatoms, including species of *Nitzschia*, *Navicula*, *Rhizosolenia*, and others. However, after the diatoms had undergone oxidation in the dark following photosynthesis, microscopic examination of the centrifuged or sedimented material revealed the presence of large numbers of Protozoa, especially certain types of amoebae, and ciliates, as well as flagellates, capable of feeding on diatoms. The bottles were also found to contain varying numbers of copepods. In the presence of such a large animal population, it seems highly probable that the effect of bacteria on the decomposition of the diatom constituents of the plankton was of minor importance. It is of interest to call attention to the suggestion of Lackey (1936) that Protozoa play an important role in the destruction of marine plant and animal residues, and also to the generally recognized role of the diatoms in the nutrition of copepods and other animal forms (Fuller & Clarke, 1936).

Discussion

The results obtained in these investigations point definitely to the fact that dead diatoms in sea water are rapidly decomposed by bacteria. In the absence of sufficient available energy, a part of the phosphate regenerated in the process of decomposition may be immediately liberated into the sea water whereas the rest, which represents the greater portion of the phosphate, is incorporated into the bacterial protoplasm as it is synthesized. Usually, however, there is an initial decrease of the dissolved phosphate due to its rapid consumption by the bacteria. The decomposition of the diatoms is accompanied by a marked increase in the bacterial population. The bacterial numbers reach a peak in a short time and then drop rapidly to low and fairly constant levels. With the death and autolysis of the bacteria, phosphate is again rapidly regenerated. Through the agency of this phosphorus cycle almost two-thirds of the phosphorus present in the dead diatoms was found in the sea water within 132 hours. In the presence of an adequate supply of available energy, all of the phosphate originally found in the sea water and also that amount which was liberated in the decomposition of the diatoms was consumed by the rapidly multiplying bacteria. But it in turn was soon regenerated into the sea water as the bacteria died and underwent autolysis.

Living diatoms, however, were not attacked by the bacterial population of the sea water. Although a greater bacterial population was usually found in the water containing living diatoms than in the untreated sea water, this increase is of a much smaller order of magnitude than that attained by bacteria in the presence of readily decomposable organic substances, as glucose or amino acids. Whereas in the breakdown of copepod plankton, a distinct parallelism was found between oxygen consumption, bacterial multiplication and ammonia liberation, in the case of the diatom plankton, no such parallelism existed. Nitrogen was liberated at a very slow rate, and the bacteria increased only to a limited extent, as compared with their numbers in the free water; this limited increase might have been due to the feeding of the bacteria on substances excreted by the diatoms or upon some of the dying diatoms.

Neither was the oxidation of freshly synthesized diatom material accompanied by active bacterial multiplication. The consumption of oxygen under these conditions was due largely to the respiration of the diatoms themselves. It seems, therefore, that living diatoms, even when photosynthesis is excluded, possess considerable resistance to bacterial attack. They are gradually consumed, however, by the animal members of the plankton. This may further account for the fact that while the process of diatom breakdown is accompanied by oxygen consumption, it is not necessarily accompanied by a parallel increase in bacterial numbers.

The authors are indebted to Miss L. Lillick, for the identification of the diatoms, to Dr C. E. Renn, for assistance in the collection of the plankton, and to Dr M. Hotchkiss for assistance in the determination of bacterial numbers.

SUMMARY

1. Dead marine diatom plankton was found to undergo rapid oxidation and decomposition when added to fresh sea water. This was measured by oxygen consumption, nitrogen liberation, phosphate regeneration and bacterial multiplication.

2. Living diatoms added to sea water and placed in the dark continued to absorb oxygen; they were rather resistant to bacterial attack.

3. Diatom-rich marine plankton also absorbed oxygen, while the phosphorus was gradually regenerated. The bacteria did not increase in numbers in correspondence with the oxidation of the fresh diatom material.

4. When sea water in which photosynthesis was allowed to proceed for varying periods of time was placed in the dark, rapid oxidation of the freshly synthesized material took place, as indicated by oxygen consumption and phosphate liberation. Although there was a greater number of bacteria in the water in which photosynthesis took place, the oxidation of the fresh diatom material was not accompanied by any large increase in bacteria; in fact a decrease in numbers was frequently observed.

5. When photosynthesis was stopped by placing the bottles in the dark, there was a marked increase in the numbers of Protozoa, notably various amoebae and ciliates, and also of copepods.

6. These results suggest that the animal forms may be largely responsible for the destruction of the living diatoms in the plankton. The role of bacteria in the regeneration of the nitrogen and phosphorus in the sea consists in the destruction of the dead diatoms as well as of the animal residues.

REFERENCES

COOPER, L. H. N., 1935. The rate of liberation of phosphate in sea water by the breakdown of plankton organisms. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 197–202.

FULLER, J. L. & CLARKE, G. L., 1936. Further experiments on the feeding of *Calanus finmarchicus*. *Biol. Bull.*, Vol. 70, pp. 308–20.

GRAN, H. H., 1933. Studies on the biology and chemistry of the Gulf of Maine. II. *Biol. Bull.*, Vol. 64, pp. 159–82.

LACKEY, J. B., 1936. Occurrence and distribution of the marine protozoan species in the Woods Hole area. *Biol. Bull.*, Vol. 70, pp. 264–78.

RENN, C. E., 1937. Bacteria and the phosphorus cycle in the sea. *Biol. Bull.*, Vol. 72, pp. 190–5.

WAKSMAN, S. A. & CAREY, C. L., 1935. Decomposition of organic matter in sea water by bacteria. II. Influence of addition of organic substances upon bacterial activities. *Journ. Bacter.*, Vol. 29, pp. 545–61.

WAKSMAN, S. A., CAREY, C. L. & REUSZER, H. W., 1933. Marine bacteria and their role in the cycle of life in the sea. I. Decomposition of marine plant and animal residues by bacteria. *Biol. Bull.*, Vol. 65, pp. 57–79.

WAKSMAN, S. A. & HOTCHKISS, M., 1937. Viability of bacteria in sea water. *Journ. Bacter.*, Vol. 33, pp. 389–400.

WAKSMAN, S. A. & RENN, C. E., 1936. Decomposition of organic matter in sea water by bacteria. III. Factors influencing the rate of decomposition. *Biol. Bull.*, Vol. 70, pp. 472–83.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1936

The Council and Officers.

Four ordinary and two special meetings of the Council have been held during the year in the Rooms of the Royal Society, London. The average attendance at the ordinary meetings was sixteen. The thanks of the Association are due to the President and Council of the Royal Society for allowing their rooms to be used. A Committee of the Council, consisting of Prof. E. W. MacBride, F.R.S., and eight other members, visited and inspected the Plymouth Laboratory on April 18.

The Council has to record with deep regret the death of Mr Howard Dunn, an Associate Member. As Chairman of the Cornwall Sea Fisheries Committee, Mr Dunn had been in close personal touch with the staff and work of the Plymouth Laboratory.

Retirement of Dr E. J. Allen.

During the year the Council learnt with the greatest sorrow that Dr E. J. Allen had decided to retire from his post as Secretary of the Association and Director of the Plymouth Laboratory. For forty-two years Dr Allen has given unremitting service to the Association, and under his wise guidance the Laboratory has risen from small beginnings to the premier position which it holds to-day. The progress which has been made and the high standard of original work which has been produced are due in a very large measure to his devotion to the interests of the Laboratory and to his gift for inspiring others with his own enthusiasm. The Council is gratified to learn that his eminent services to science have been recognized by the award of the Darwin Medal of the Royal Society.

The Plymouth Laboratory.

Somewhat heavy repairs and replacements have proved necessary during the year to maintain the Laboratory buildings and fittings in satisfactory condition. The whole of the electric light wiring of the main building has been renewed. The fire-chamber of the furnace of the central heating plant of the Laboratory has been rebuilt, and a considerable length of the hot-water piping leading underground to the North Building has been replaced. Corroded supply pipes connected with the electric pumps used for circulating sea water through the aquarium and laboratory tanks have been replaced by larger ones (3 in. diameter in place of 2 in.) which are glass-lined. One of the two electrically driven air pumps for supplying air to the Aquarium and Laboratory has completely broken down; it has been replaced by an air blower supplied by the British Vacuum Cleaner and Engineering Co., Ltd., guaranteed to deliver up to 60 $ft.^3$ of air per minute at a pressure of 3 lb. External painting of the Main and North Buildings has been carried out where necessary.

It has been found necessary to make some alterations to the Director's house and to redecorate it throughout. Part of the cost is being defrayed from the Association's funds and part from a special grant made for this purpose from the Development Fund.

The Aquarium.

The Aquarium tanks have been well stocked throughout the year and in them a thoroughly representative living collection of the local marine fauna has been maintained. The table-tanks down the centre have been provided with anti-splash pipes, which, while not interfering with circulation of the water, prevent ripples forming on the surface, thus giving greatly improved visibility. The number of visitors has reached a high average, and as in former years, numerous parties of pupils from schools and other educational institutions have paid profitable visits.

The Ship and Motor Boat.

The steam drifter *Salpa* and the motor-boat *Gammarus* have worked continuously throughout the year, except for brief periods occupied by the normal refits necessary for their proper upkeep. Most of this work has been done, as usual, by the vessels' own crews.

On October 19 the *Salpa* entered the yard of Messrs Philip and Son, Dartmouth, in order to undergo Lloyd's full-time survey and reconditioning. The hull was found to be in excellent condition. Repairs have proved more extensive than was expected; it has been necessary to lift out the main engine in order to replace the badly corroded bolts which secure the engine bearers.

As anticipated in last year's report, the 6 h.p. Kelvin-Ricardo engine of the *Gammarus* has become increasingly troublesome and an extensive overhaul, including the fitting of new cylinders, is now necessary.

The Staff.

Dr Stanley Kemp has been appointed Secretary to the Council and Director of the Plymouth Laboratory in succession to Dr E. J. Allen who retired on September 30 1936. Dr Kemp took up his post on October 1.

Mr D. P. Wilson was promoted to the grade of Naturalist in April.

Mr W. J. Rees joined the staff of the Plymouth Laboratory in January as Research Assistant to work on hydroids and medusae. His salary is provided from a special fund kindly contributed for this purpose by Mr E. T. Browne.

Mr P. G. Corbin joined the staff of the Plymouth Laboratory in August as Mackerel Research Assistant, and is taking part in the programme of work which has been drawn up in conjunction with the Ministry of Agriculture and Fisheries.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year:

Dr Z. M. Bacq, Liège (Acetylcholine in invertebrate muscle).
Miss M. G. Barnes, Cambridge (General Zoology).
Dr E. J. W. Barrington, Oxford (Digestion in *Amphioxus*).
Dr R. Bassindale, Manchester (Barnacle morphology and development).
Dr G. B. Bhalerao, Muktesar, Kumaun, India (Helminthology).
Dr A. M. Bidder, Cambridge (Cephalopods).
Dr R. Biebl, Vienna (Cell physiological studies on red algae).
Dr J. Y. Bogue, London (Conduction in non-medullated nerve of *Maia*).
Dr G. J. Broekhuysen, Jr., Rijswijk, Holland (Breeding habits of *Carcinus maenas*).
Dr I. Chang, Shanghai, China (Conduction in non-medullated nerve of *Maia*).
Dr G. L. Clarke, Woods Hole, U.S.A. (Library).
H. A. Cole, Conway (Culture methods).
J. S. Colman, Farnham (Library).
Prof. E. G. Conklin, Princeton, U.S.A. (General Fauna).
G. I. Crawford, London (Marine Mollusca).
L. R. Crawshay, lately Officer for Sponge Research, British Honduras (Sponges).
P. R. Crimp, Sheffield (Microfauna).
J. F. Danielli, London (Properties of the plasma membrane).
T. Davidson, London (Photography of marine animals).
H. Davson, London (Library).
Miss M. J. Dibb, London (Parasitology).
Dr F. Fessard, Paris (Stretch receptors in fish muscle).
Prof. R. A. Fisher, London (Library).
R. R. Fowell, London (Oocysts of a coccidian from *Polydora flava* and gregarines in trematodes. Suctoria of Tunicates).
Dr V. Fretter, London (Chiton. Excretion in Molluscs).
Miss N. Frost, Newfoundland (Plankton).
Miss E. G. Geiler, Southport (General Biology).
Prof. E. S. Goodrich, Oxford (Development of *Phascolosoma vulgare*).
Dr H. L. M. Pixell-Goodrich, Oxford (Parasites in *Phascolosoma minutum*).
Dr A. Graham, London (Digestion in Gastropods).
Dr J. Gray, Cambridge (Locomotion of Polychaetes and Molluscs).
Dr F. Gross, Vienna and Berlin (Culture of marine organisms).
Dr R. Gurney, Oxford (Decapod larvae).
D. M. Hall, Cambridge (Library).
Dr and Mrs F. R. Hayes, Halifax, Nova Scotia (Inorganic salts in Molluscs).
H. H. Howells, Bristol (Digestive processes in the Tectibranchs).
Miss P. M. Jenkin, Bristol (Diatoms).
Miss M. W. Jepps, Glasgow (Protozoa).
Dr P. Jespersen, Copenhagen (Plankton, especially Copepods).
J. H. Johnston, Cambridge (General Zoology).
Dr B. Katz, London (Neuromuscular system of Crustacea).

Dr J. A. Kitching, London (Physiology of Protozoa).
Dr H. Koch, Louvain (Physiology of the swim bladder).
Dr F. H. Liu, London (Mackerel research).
Dr A. M. Lysaght, New Zealand (Larval Gastropods).
A. Milne, Aberdeen (Estuarine fauna).
Dr H. B. Moore, Plymouth (Littoral Ecology).
Dr D. Nachmansohn, Paris (Nerve and muscle metabolism).
Dr A. G. Nicholls, Millport (Sand Copepods).
J. A. Nicholson, Bristol (Ecology of a salt marsh).
Dr C. L. Oakley, London (Parasitic Copepods).
Dr and Mrs C. F. A. Pantin, Cambridge (Chemical action and facilitation in Actinozoa).
Dr Hans Pettersson, Göteborg (Light measurement).
Dr H. H. Poole, Dublin (Photo-electric measurements of light).
F. A. Potts, Cambridge (*Pomatoceros*).
J. M. Reynolds, Leicester (Pycnogonid development).
Dr H. Rosenberg, London (Conduction in non-medullated nerve of *Maia*).
E. P. Rutenberg, Moscow (Fisheries and methods of marine research).
A. Sandison, Cambridge (Proprioceptive reflexes on *Carcinus*).
Prof. P. B. Sivickis, Lithuania (Regeneration).
J. E. Smith, Sheffield (Library. Nervous system of Asteroids).
Miss N. G. Sproston, London (General Zoology and Parasitology).
Miss F. A. Stanbury, Plymouth (Artificial culture of diatoms).
Dr Helge Thomsen, Copenhagen (Hydrography).
T. G. Tutin, Kew (*Zostera*).
Dr G. Vandebroek, Ghent (Embryology of Ascidians).
G. P. Wells, London (Physiology of *Arenicola*).
Miss U. Wykes, Oxford (Colour-change in fish).
F. Yates, Rothamsted (Library).

The annual Course in Marine Biology was held as usual during the Easter Vacation, conducted by Mr D. P. Wilson and Mr G. A. Steven. It was attended by forty-two students from Oxford, Cambridge, London, Edinburgh, Sheffield, Liverpool, Leeds, Birmingham, Nottingham, Bristol, Exeter, and Plymouth.

During the Summer Vacation a Course of Marine Biology was conducted by Prof. J. H. Orton, assisted by Miss Ruth Rawlinson as Demonstrator. This was attended by twenty-one students from Oxford, Cambridge, London, Birmingham, Nottingham, Bristol, and Dauntsey's School, West Lavington.

Also during the Easter Vacation, Mr J. M. Branfoot brought three students from Oundle School; Mr P. H. White, three from Harrow; Mr H. C. W. Wilson, four from Monkton Combe; Mr H. C. Wallwork, two from Highgate School; Mr A. H. Lewis, six from Wellington College; and Mr A. H. Pott, four from Bradfield College

At Whitsuntide a class of five students was conducted by Dr E. Idris Jones of the Chelsea Polytechnic, and a botanical class held by Dr A. R. Clapham and Dr and Mrs W. O. James during the Easter Vacation was attended by eight students from Oxford University.

In September the new French Research Vessel, *Président Théodore Tissier*, with Dr Ed. le Danois and Prof. Perez, paid a visit to Plymouth.

The Scientific Work of the Plymouth Laboratory Staff.

Physics and Chemistry of the Environment

Dr H. H. Poole has continued his collaboration with Dr W. R. G. Atkins upon the photo-electric measurement of illumination. Dr Poole visited Copenhagen and contributed a paper on methods of measurement to the special meeting held in May. A subcommittee was appointed to draw up an outline of the most serviceable equipment for the routine measurement of submarine illumination. They were both invited to the Oxford meeting of the International Radiation Commission in September and the subcommittee met there. A draft report is being circulated. Further work has been carried out at Plymouth upon the penetration of the different parts of the spectrum.

Photo-electric cells have been standardized for other workers and used in connexion with the culture of diatoms and the survey of the littoral fauna and flora.

The work upon the photo-electric measurement of the luminous efficiency of daylight, which was mentioned in last year's Report, has been published; in this the luminous efficiency of animal light has been briefly compared with that of other natural and artificial sources.

The measurement of the energy received from any source in different parts of the spectrum is, for various reasons, peculiarly difficult to carry out. Under the special conditions of open-air work photo-electric cells have certain advantages over thermopiles. A method has been developed by which cells, used with colour filters, have been standardized to measure energy in microwatts per square centimetre per microampere of the photo-electric current. Measurements have thus been made of the "spectral power density", in milliwatts per sq. cm. per millimicron, for sunlight, sky light and mixed daylight. Experience has been gained as to the most suitable cells and filters by working on shore, on the Laboratory roof and in woods; in the latter the colour composition of the light has been altered by the passage of some of it through leaves, the transmission of which was studied separately. In a portion of this work Miss F. A. Stanbury collaborated. It has been published in the Proceedings of the Royal and Royal Dublin Societies. As a result it will now be possible to give, not only the spectral composition of the light at any depth in the sea, but also, with approximate accuracy, the energy in broad spectral bands.

Further work on tropical daylight has been carried out by Prof. N. G. Ball, in Ceylon, by means of photo-cells standardized here. A paper is being prepared embodying these results as compared with similar measurements at Plymouth. It is possible that results obtained in Greenland by Mr Wager of Trinity College, Dublin, may also be ready in time for inclusion. They also were carried out with a standardized cell.

Arising out of his previous work on the quantitative estimation of copper and zinc in sea water, Dr Atkins has been able to study the corrosion of certain metals and alloys by a method which gives rough quantitative results quickly; information may thus be obtained as to the probable suitability or unsuitability of various alloys for use in connexion with aquaria. Dr Atkins was also concerned in the revision of the memorandum of the International Commission dealing with "The Reporting of Oceanographic Chemistry".

Dr L. H. N. Cooper has devoted attention to the significant role of copper in the so-called salt error in phosphorus determinations in sea water. An attempt has been made to evaluate the effect of the error on past work in order to prepare a survey of the changes in phosphate concentration off Plymouth in the last 16 years. The years 1932–5 stand in marked contrast to the earlier years, for not only was the available phosphate much reduced but even the smaller amount present was less efficiently used. The year 1935 was the worst of all with lowest available phosphate and lowest percentage utilization. Furthermore, the phosphate fluctuations run very closely parallel with fluctuations in the production of young fish and the essential dependence of the biological stock upon the stock of nutrients is becoming ever more clear.

Work on the organic phosphorus content of sea water has shown that this is not large and probably of no great importance and further that about one-half of the organic phosphorus that has been variously reported is not phosphorus at all but arsenic.

As a result of Mr Harvey's investigations upon the assimilation of iron by diatoms, Dr Cooper resumed his study of iron in sea water. Owing to the great insolubility of ferric hydroxide and the minute amounts of iron present, the field has been first surveyed from a purely theoretical thermodynamic standpoint, which has necessitated a study of the oxidation-reduction potential of sea water. The reversible oxidation-reduction potential due to oxygen in solution is not greatly affected by changes in temperature, pH and degree of saturation of oxygen within the limits occurring in natural sea water, but owing to the peculiar irreversible nature of the oxygen system, the theoretical reversible potential can never be measured, and in addition the water is likely to be poorly poised. Measurements of the potential made by Dr Atkins agree with what would be expected of the irreversible potential of an oxygen system and show clearly that there is no other system able to impart poise to sea water. From these results it would now seem that not more than 10^{-7} mg./m.^{3} ferrous iron can exist in equilibrium in natural sea water. Since diatoms have been found to contain reactive ferrous iron, their cell substance must have a negative oxidation-reduction potential and the readiness with which iron can be assimilated will depend mainly on the potential of the cell wall. Consideration of the iron system from the point of view of oxidation-reduction potential has served to co-ordinate many scattered observations and promises to be of real value in providing a comprehensive viewpoint from which to direct further research.

Hydrographic data have been collected in the mouth of the English Channel during the year. In February water of unusually low salinity was found north of Ushant; in April this had penetrated as far as the neighbourhood of Plymouth, filling the whole mouth of the Channel with water of 34·5 to 34·6 °/₀₀ salinity. The incursion appears similar to those which occurred in the spring of 1928 and 1931, but the incoming water was of lower salinity.

Plankton

Mr Harvey has investigated the growth rate (rate of division) of the diatom *Biddulphia mobiliensis* under known constant conditions of light and temperature. A series of experiments showed that the conditions under which the diatom had lived during the previous week had a marked influence upon its growth rate at optimum light intensity and upon the light intensity which was optimum. Furthermore, a rise in temperature from 13 to 18° C. caused an increase or a decrease in growth rate, dependent upon both the light intensity and the conditions under which the diatoms had lived previous to the experiment.

The growth rate of this species was then followed over a period of 6 weeks and sixteen divisions at 13° C. and 7400 metre candles, in order to see if it would attain a constant rate under such conditions. The population was kept between 100 and 350 cells per c.c. by diluting at intervals. It had previously been found that the growth rate per hour in light at this intensity was the same whether the light was continuous or alternating with periods of darkness. It was also found that the rate was not appreciably affected by population densities between 100 and 550 cells per c.c., provided they were in fresh culture medium. Throughout the 6 weeks the growth rate of the diatom population fluctuated. The fluctuations were irregular, greater than experimental sampling errors which were calculable, and appeared to be independent of the population density at the time. Secondary experiments indicated that the fluctuations were due to variation in the amount of iron in a form available to the diatoms.

It was apparent that uniform reproducible results from experiment to experiment, as distinct from duplicate results in the same experiment, would not be obtained unless the diatoms were supplied with iron in similar quantities and equally available.

Information was then sought concerning the form in which iron is utilized by diatoms; experiment showed them to be rich in ferrous iron. Ferric hydroxide or phosphate in sea water was found to give off ferrous ions in sufficient quantity to form, slowly, enough red ferrous dipyridyl to be apparent. There was no reason to suppose the ferric iron in solution (10^{-12} mg./m.^{3}) had been reduced by the dipyridyl. Dr Cooper then took up the question of how much ferrous iron could exist in solution in sea water of *p*H 8. From the calculated oxidation-reduction potential of aerated sea water, the value of which was further checked by Dr Atkins, it appears that less than 10^{-7} mg./m.^{3} of ferrous iron can exist in equilibrium, any amount in excess becoming oxidized and precipitated as ferric hydroxide. A single diatom contains as much iron as can exist in solution in a cubic metre of sea water. No diatom growth could be obtained in culture media (Allen-Miquel and iron citrate) which had been passed through a membrane filter unless some of the residue was added to the filtrate.

These considerations suggest that diatoms dissolve particles of ferric hydroxide—or ferric phosphate in the case of Allen-Miquel culture medium—with which they come in contact. It presupposes either that the *p*H at the diatom-water interface is less than that in the water or that the oxidation-reduction potential at the interface is lower than in the water. The cell *contents* were found to be at or below *p*H 6 and are known to be at a relatively low oxidation-reduction potential. As a consequence the efficacy of various suspensions of iron hydroxide in sea water will vary with the readiness with which the particles dissolve in dilute acid or give off ferrous ions in a medium of low oxidation-reduction potential.

Suspensions of ferric hydroxide or phosphate were found to dissolve at a *p*H between 5 and 6, provided the product of solution was removed from the sphere of action—as by forming a citrate complex or the dipyridyl compound after reduction. The rate of solution varied greatly with suspensions formed in different ways. In general they were readily soluble soon after being formed, and became only slowly or partially soluble with age. Experiments, as yet incomplete, indicate the more soluble suspensions to be more effective in increasing the growth rate of diatoms.

Dr Cooper has started an investigation on the ultimate chemical composition of plankton organisms in order to close a gap in our knowledge of the food chain in the sea. Satisfactory micro-analytical methods have now been worked out for carbon, phosphorus, nitrogen, iron, copper and manganese, and these have been applied to a number of animal samples during the last year, including *Sagitta elegans*, ctenophores, crab zoeas and young *Callionymus*. Sampling technique, however, still requires improvement. The larger plankton animals are fairly easily handled, but the smaller zooplankton and the phytoplankton demand improved methods. Thus carefully checked analyses on *Balanus* nauplii supplied by Dr Moore showed that, due to imperfect sampling, errors of as much as 20 % could creep into results obtained on apparently well-mixed material. It is too early to draw extensive deductions, but already it appears that manganese, known to be of considerable importance in the metabolism of many terrestrial plants and animals, plays no part in the sea.

Mr F. S. Russell has continued his weekly examinations of plankton with special reference to the occurrence of certain indicators of water movements. In connexion with this work the results of the 1935 cruise on Col. E. T. Peel's yacht, *St George*, were published in Volume xx, No. 3, of the *Journal*. These results gave a clear indication that certain plankton organisms would prove of use in studying the changes in the water off Plymouth. The year 1935 was characterized by a predominance of *Sagitta setosa* and almost complete absence of *S. elegans* and its associated indicators. A review of these researches up till 1935 has been published in the *Rapports et Procès Verbaux*, Volume 100, of the International Council, and was read before the Atlantic Slope Committee at Copenhagen.

The year 1936 has shown rather unusual conditions. Neither *S. setosa* nor *S. elegans* have been present in numbers and there have been indications of the presence of oceanic water in the occurrence of such animals as the Scyphomedusa *Pelagia*. The reappearance of the Siphonophore *Muggiaea atlantica* is also noteworthy. This species had been replaced by *M. kochi* in 1925, which has now itself been once more replaced by *M. atlantica* after a period of ten years. The detailed analysis of the results is not yet completed.

During the examination of the weekly ring-trawl catches of plankton the counting of all the medusae has been continued, and observations made on the growth of certain species. These observations have now extended over a period of 6 years and a paper on the results is nearing completion.

In May Mr Russell attended the meeting of the International Council for the Exploration of the Sea at Copenhagen, where he had been invited to lecture on "Submarine Illumination in Relation to Animal Life". This has since been published. In September he attended the meeting of the International Union of Geodesy and Geophysics at Edinburgh where he read a paper on plankton indicators.

Dr M. V. Lebour has been mainly studying the lamellibranch larvae of the plankton, having published in March in the Association's *Journal* a general paper on prosobranch larvae. There are a great many veligers of lamellibranchs both in the inside and outside waters, and they are almost unknown. It is found that the greatest number breed in late summer and early autumn, but certain very common forms, breeding at other times, result in the presence of a quantity of veligers of some kind or another throughout the year. Thus the veligers of *Mytilus* characterize the plankton in May and June, those of *Ensis* in late winter and early spring, *Anomia* (*Heteranomia*) and *Lima* in autumn and winter. The abundance of lamellibranch veligers shows clearly that they are of great importance economically and well worth study.

The veligers are picked out from the fresh plankton samples and reared in bowls or plunger-jars, the latter being the more successful, and fed with diatoms and flagellates until they lose the velum and grow to a stage at which the species, or perhaps the genus only, can be recognized. At the same time the gonads of as many adults as possible are examined in order to establish the breeding seasons and, whenever possible, to attempt fertilizations. Some of these fertilizations have resulted in bringing the eggs as far as the shelled stage, a few growing to the end of the veliger stage and metamorphosing. In this way *Cardium edule* and *C. nodosum* have been reared in bowls as far as the crawling stage, and four species of *Cardium* have been identified in the plankton. The most striking of all the lamellibranch larvae is *Lima*. Its veliger shell is wedge-shaped and unlike any other, and in its later stages the foot is twisted so that it moves with the mouth behind it. In the plunger-jar, after losing the velum, long tentacles grow out from the mantle which aid in the movement, the animal crawling hinge downwards, the foot moving like a leech, the tentacles widely extended. A species of *Ensis*, almost certainly *E. siliqua*, has been reared from the veliger to a size in which the genus can be recognized, showing it to be one of the commonest in the plankton in winter and early spring, the adults all being ripe in March, when extensive collections were made, and quite spent in late summer. It is found that sometimes the smaller species, such as *Kellia suborbicularis*, have veligers which greatly exceed in size those of some of the larger forms.

Plankton samples are continually examined for their larvae, and any unusual gastropod or crustacean larvae noted. In October of this year a *Lamellaria* echinospira larva, not seen before, was found in the townets. This probably belongs to an oceanic species not living in the Plymouth district.

In May a paper on the two species of *Spirontocaris* at Plymouth, one being new, and their larvae, was published in the *Proceedings of the Zoological Society*, and in October a paper on the two Plymouth species of *Processa* and their larvae was published in the same periodical. In this latter paper two species are recognized though it had hitherto been thought that there was only one in this district.

Mr Russell has spent much time this year on his work on a monograph of British Medusae in collaboration with Mr E. T. Browne. He has twice visited Mr Browne on his kind invitation to Berkhamsted. The preliminary typescripts of fifteen species of Anthomedusae have now been completed. The various stages of a new species of *Eucheilota*, the medusa of *Lovenella clausa*, were described in Volume xx, No. 3, of the *Journal*. It has been found that if fragments of dredged material are left for several days in bowls of pure sea water various species of delicate hydroids will develop whose hydranths are probably damaged while being caught. In connexion with this work Mr Russell has received much assistance from Mr W. J. Rees and together they have reared and followed through the life-histories of the hydroid *Zanclea implexa* and its medusa. This hydroid has been found constantly in association with an encrusting polyzoan. The report on these observations has been published in Volume xxi, No. 1, of the *Journal*.

Mr W. J. Rees has been working on the life-histories of Plymouth medusae. Young hydroids have been reared by fertilization in the laboratory from the medusae *Turritopsis*, *Amphinema dinema*, *Octorchis gegenbauri* and *Corymorpha nutans*. Colonies of various hydroids have been kept alive in the laboratory in the hope that they would produce medusae and by this means several life-histories have been confirmed. The keeping of these colonies in a healthy living state has entailed much time and care as they must be kept clean and well fed. At times polyps have required individual feeding.

Fauna of the Sea Floor (Ecology, Physiology, Genetics)

A hydroid colony reared by Mr Rees from a single stolon, at first thought to be *Stauridium productum*, proved to be a new species of the genus *Staurocoryne*. An account of this new species, *Staurocoryne filiformis*, has been published in Volume XXI, No. 1 of the *Journal*.

In July a small *Corymorpha*-like hydroid was found on a hapteron of *Laminaria digitata* which during its short life exhibited a peculiar process of asexual reproduction. A kind of inverted bud-formation occurred in which the oral tentacles were situated near its point of origin, instead of at its distal extremity which became the hydrocaulus. On liberation the bud attached itself but only lived a few days.

During the year two trematode papers have been published by him on work done in part at Plymouth.

Owing to the difficulty of dealing with soft muds, little information exists on the nature and density of the inter-tidal mud-fauna. Dr H. B. Moore having devised a method of sieving, effective even for the most adhesive of muds, the opportunity was taken by Mr G. M. Spooner to work in collaboration in procuring material to provide a basis for such a study. Mr Spooner has dealt with this material, having sorted out and counted the macroscopic fauna from fourteen stations on the expansive mud flats of St John's Lake, at the mouth of the Tamar, and other stations from Poole Harbour, Dorset, giving an estimate of the density of different species at various tidal levels.

Statistical examinations which have been made by Mr Spooner of data procured by workers at the Laboratory include the testing of correlations between various measurements of shell characters and environmental factors of local populations of the mollusc, *Purpura lapillus*. (The measurements are those of Dr H. B. Moore, who has used the results in his paper published in the November issue of the *Journal*.)

The work on the horizontal semicircular canal of the dogfish, begun last year by Dr A. Sand in collaboration with Dr O. Löwenstein of Birmingham, has been completed and published in the *Journal of Experimental Biology*, Vol. XIII, No. 4. This investigation has led to a new interpretation of the significance of spontaneous activity in a sense organ. The horizontal ampulla was found to maintain a spontaneous discharge of afferent impulses in the nerve branch supplying it. This was increased during ipsilateral rotation, and abolished during contralateral rotation. Each of the two horizontal ampullae is therefore able to discriminate left and right displacement, and the two together, in the intact animal, work antagonistically, and constitute a mechanism which is twice as sensitive to angular displacement as each individual ampulla by itself. Dr Sand also carried out an investigation on the muscle proprioceptors of the ray, in collaboration with Dr A. Fessard of Paris. No histological or physiological evidence has hitherto existed of the presence of stretch receptors in the muscles of fishes. The pelvic fin muscles of the ray provided a preparation from which the afferent nerve impulses arising from a single end organ could be recorded electrically. Various aspects of the behaviour of the sense organ, such as the relation of tension to frequency of discharge, adaptation to a constant load and effect of a temporary overload, were analysed. The results are being prepared for publication.

During the year, three papers have been prepared by Mrs E. W. Sexton and Miss A. R. Clark, and published in the *Journal* of the Association, reporting on the breeding experiments in *Gammarus chevreuxi*. The most important is an attempt to summarize the whole work which has been carried on since 1912. This account is fully documented, giving references to all the previous papers on heredity in this species, including that done by other workers on material which has originated from Plymouth.

The principal subjects dealt with include descriptions of conditions under which the animal lives in the wild, of its moulting and development, and special consideration has been given to the question of telegony. The different mutant characters as they appeared in laboratory cultures are recorded and the history of each is summarized. A detailed account is given of certain preliminary experiments made for the purpose of studying the effect of temperature on the rate of development of the eggs and young and to find out whether or not temperature can be a factor in the production of mutations.

A fuller account is given of the experiment made in 1931, which has already been referred to in a letter to *Nature*. In this, there occurred changes in body-colour; changes in the retinal eye-colour with the reappearance of certain previously known genes; the appearance of three other red-eyed recessives, as well as of two quite new recessive types, the Lilac-eye and the Nowhite-Red; and finally, changes in the interommatidial white pigment. The first appearance of the Clotted-eye is recorded; in this type the white pigment assumed many shapes from regular reticulation to superficial clotted masses in the eye and spots on the head.

The Clotted-eye and its inheritance is treated more fully in the second paper, "Variations in the white pigment of the eye in *Gammarus chevreuxi* Sexton, with a description of a new genetic type, the Clotted-eye".

The third paper, based on experiments made in 1933, deals with another aspect of the researches, viz. definite experimental proofs of the occurrence of heterozygotes in the wild population of *G. chevreuxi*. In two cases, pairs of black-eyed animals from the wild, kept in the laboratory till the eggs hatched, gave some red-eyed offspring in the F_1 showing that both the parents in each pair must have been heterozygous in constitution. That this conclusion was correct was proved later (1935) by the appearance of a red-eyed recessive in the wild—taken in a dredging with 2040 black-eyed animals.

In connexion with the occurrence of heterogeneity in the wild population of *Gammarus chevreuxi*, which Mrs Sexton's work has now established, Mr Spooner has analysed Mrs Sexton's figures in order to obtain an estimate of the proportion of animals carrying recessive genes in their natural conditions.

Fish and Fisheries

The drift-net fishery for herrings at Plymouth during the winter of 1935–36 was followed by Mr E. Ford. East Country steam drifters, numbering 105, landed a total weight of 33,847 cwt. in the two months December, 1935, and January, 1936, with an average landing for the season of 16·2 cwt. This result was poor enough, but it was far better than the distressing failure of the motor drifter fishery, which yielded no more than 1172 cwt. during the same period. Only 38 motor drifters from Cornish ports participated in the fishery, as against 59 in the previous season, and their average landing for the season was only 7·1 cwt. This result forms a striking contrast with that of, say the season 1929–30 when 169 Cornish drifters made an average landing of 42·5 cwt. Once again, big old fish predominated in the catches, there being a continued dearth of herrings under 6 years of age. As explained in last year's Report the comparative absence of young fish in the shoals during recent years is as yet inexplicable, but there seems no doubt at all that it has seriously affected the yield of the Plymouth winter fishery.

In connexion with Mr Ford's study of variation in the vertebral column of teleostean fishes, further specimens have been prepared and examined with a view to increasing the data on variation from individual to individual of the same species.

Mr Ford was appointed the Buckland Professor for the year 1936. He delivered the first series of three lectures at Plymouth in the spring of the year, and the second series in London at University College during November and early December. His subject was "The Nation's Sea-Fish Supply".

During the first part of the year Mr G. A. Steven continued his researches on the rays and skates of the English Channel. A paper embodying his latest results—"On the Migrations and Growth of the Thornback Ray"—was published in the Association's *Journal* in March last. The non-migratory habit of the young of this species is confirmed and further data on their growth-rate have been collected. Both sexes grow at about the same rate—approximately 6 cm. per annum—until the males reach sexual maturity at about 7 years of age. The average age of the females on reaching first maturity is approximately 9 years.

An unusually interesting record was obtained on October 2 1936, when a Thornback which had been marked and liberated on December 23 1931 (almost 5 years previously) was returned to the Laboratory. When marked it was a small immature male of only 27 cm. disk width; when recaptured it had reached a width of 54 cm., was fully mature sexually, and in excellent body condition.

During the remainder of the year Mr Steven, assisted by Mr P. H. T. Hartley and later by Mr P. G. Corbin, has been fully occupied with the initiation of an investigation into the biology of the mackerel in western waters.

Systematic examination of samples of mackerel for length, sex, sexual condition, stomach contents and age have been carried on throughout the summer. Over 1150 fish have been examined, but scales have been collected from only about 300 fish which were wrapped in paper immediately on being caught by hook and line. It has been found impracticable or even impossible to collect scales from ordinary samples of fish landed on a fish market because of the extreme smallness of the scales which are very easily dislodged. Moreover, only a very small proportion of the scales have any ring markings upon them. If, however, a sufficient number of scales—i.e. *a few hundreds*—from each fish be examined, some scales with clear ring markings can usually be obtained. Whether or not these rings are annual rings of growth cannot as yet be determined. This will probably not be possible until the young stages, from about ½ in. up to about 6 in. in length, can be obtained in quantity for examination.

Because of the difficulty of obtaining scales, otoliths have been collected from every fish examined. It is found that rings can be counted in otoliths from the younger—i.e. smaller—fish, and that these agree with the scale markings, where scales have been obtained. As with the scales themselves, however, interpretation of the otolith readings is not yet possible.

Four cruises in the S.S. *Salpa* and two trips in commercial fishing vessels have been made in search of mackerel larvae and general plankton samples. The plankton and young fish collections have been worked up by Mr Hartley and Mr Corbin. On April 29 a few larvae were taken in townets in deep water at and beyond the mouth of the Channel. This appears to be the earliest record ever obtained of the presence of mackerel larvae in these waters and points to spawning activities at least as early as mid-April. The larvae were most abundant in June, after which their numbers decreased and by September they had entirely disappeared.

Mr F. S. Russell has continued his observations on the seasonal abundance of the pelagic stages of young fishes. A report on the year 1935 was published in Volume xx, No. 3, of the *Journal*. The collections in 1936 have shown that the year has been in some respects even worse than 1935; there has, for instance, been an almost complete absence of the normal peak of young of spring spawners. This was again associated with low phosphate values in the preceding winter. There was, however, evidence of improvement in the numbers of the young of summer spawners; this may possibly prove to have some relation with the presence of oceanic water. The year was remarkable for the numbers of pilchard eggs, which have lasted in the plankton from the end of March until October.

In June and July Mr Russell took part in two of the cruises in the S.S. *Salpa* for a study of the distribution of plankton and young fish in the mackerel investigation programme.

The work begun last year by Mr D. P. Wilson on the histologically stainable fat in the non-visceral parts of fishes has been continued. A simple method of handling large hand-cut slices of fish has been used. After staining in Scarlet

Red the fat depots are clearly visible. In a few cases thin sections have been cut on a freezing microtome in order to observe more clearly the histological details. Most of the local flat-fishes (Pleuronectidae and Soleidae) have been investigated and they all closely resemble one another. There are generally a few scattered fat droplets between the skin and the underlying muscles, while a layer of fatty tissue is frequently developed between the superficial lateral and deep lateral muscles. There is a considerable amount of fat associated with the skeleton; the interstices of the spongy parts of the centra may be loaded with fatty tissue. A larger quantity of fat, however, is stored around and between the muscles which move the rays of the dorsal and ventral fins. The gaps between these muscles are occupied by a spongy connective tissue heavily impregnated with fat.

The gadoids form a contrast to the flat-fishes, as in them little or no stainable fat is to be observed. The hake is, however, a rather striking exception in that the superficial lateral muscle contains minute fat droplets intracellularly in the muscle fibres. In most of the other fishes investigated this muscle, if it holds fat at all, has it in the form of intercellular drops. The salmon is an instance of another species containing intracellular fat in the fibres of this muscle.

In some fishes a thick layer of fat occurs immediately below the skin, as in the red mullet and some gurnards, and also in the herring, where it has long been known. These species like the flat-fishes have some fat associated with the skeleton and around the muscles of the median fins. *Cepola rubescens* is an example of a fish with skeletal and fin-ray muscle fat, but with none apparently under the skin.

There is evidently a certain amount of individual variation in fat content between fishes of the same size and species; there may also be seasonal variation, but this is not very clear. There is some evidence that plaice immediately after spawning lose some or all of their non-visceral fat, but this has not yet been fully established.

Observations on the habits of the angler-fish, *Lophius piscatorius*, have been continued and much interesting information obtained. A search of the literature has revealed that this species has scarcely ever before been watched alive, and in perfect health, either in the sea or in aquarium tanks. The longest-lived fish was kept for eleven months and several others for periods exceeding three months. Growth was at an average rate of about eight and a half inches per annum. The angler-fishes dug for themselves hollows in the sand and settled down therein. The tags of skin bordering their bodies rested on the surrounding surface and to the eye broke up the outlines of the fishes most effectively. The colour and mottlings would be at the same time closely matched to the substratum, altogether rendering the fishes extremely difficult to detect. Breathing movements occurred only once every one or two minutes, so there was very little movement to reveal where they lay, and in general other fishes in the tank did not readily perceive them. The lure was at times most definitely used to attract fishes within seizing distance. Gadoids, clupeoids, and similar soft-finned round fishes were readily eaten, but flat-fishes were taken only occasionally. Some species, notably those with spines, were not eaten. There appeared to be a size discrimination, fishes longer than the width of the angler's mouth rarely being swallowed. A paper recording these observations has been prepared for the press.

Mr G. M. Spooner has written up the results of experiments on the learning abilities shown by the wrasse, on which a paper will be published in the next number of the *Journal*. The fish were trained to make detours to reach their food, and the method by which they came to develop an efficient response investigated. The main feature which has emerged is that the learning shown by the fish proved not to be of the nature of a motor habit, and can only be accounted for if it is supposed that the fish acquired a more adequate perception of their surroundings which enabled them to give a more effective response.

The learning of detours by teleost fish appears to rest essentially on the same footing as problem-solving behaviour in higher vertebrates, a form of organic activity which presents considerable difficulties to orthodox biological theory. Mr Spooner is about to continue behaviour experiments on these fish and other marine animals to establish points which have arisen out of this work.

In November 1935, an investigation of the tuck-net fishing in the estuaries of the Tamar and Lynher was begun by Mr P. H. T. Hartley, and frequent fishing expeditions to these rivers have been made. Hauls have been made with an ordinary tuck-seine belonging to a Saltash fisherman, and also with a special seine fitted with a French netting cod-end. The valuable fishes caught in the tuck-net are flounders, plaice, and bass. Dabs and small gadoids are present in large numbers, but few are large enough to be valuable. Some herring are netted in winter. The estuary fishermen use the tuck-net chiefly in winter; catches made in the summer are very small. Between March and August the fishing is for salmon in the upper tidal reaches, with large-meshed nets. Unless the water is very muddy, night fishing yields larger hauls than day fishing.

Samples of fish of all species present in the estuaries have been measured each month, and stomach contents examined. It has been found that flounders feed almost exclusively on Crustacea, especially *Crangon vulgaris*. Dabs feed chiefly on *Spirographis spallanzani*, except in their first year, when their diet is mixed small polychaetes and Crustacea. Plaice are mixed feeders, but take rather more Polychaeta than Crustacea.

The results obtained, since 1930, upon the preservation of fishing nets have now been published by Dr Atkins, and Prof. J. Purser of Trinity College, Dublin, collaborated with him upon methods for the preservation of fibre ropes. Good preservation was obtained with some of the mixtures. Thus untreated, thin manila rope had fallen to 13 % of its initial strength after 10½ months in the Cawsand Fish Pool. Certain preservatives kept it up to at least 70 %. Under Plymouth Pier 2 in. ropes of hemp and manila became rotten in one year; various mixtures prevented this, so that the ropes gave 60–97 % of their initial tensile strengths. Advisory work on the preservation of nets and ropes has been continued. Several large firms have now become interested and are conducting extensive trials with nets issued to fishing boats.

Experiments with anti-fouling compositions in co-operation with a firm of paint manufacturers who have supplied the test compositions with which the *Salpa* has been coated, have been discontinued for the time being. A final report was submitted to the paint company in July.

The testing of the resistance of various timbers treated with Cuprinol, and of the insulating materials for marine telegraph cables, has again been carried out, and reports tendered.

The Library.

The thanks of the Association are again due to numerous Foreign Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the *Journal*. Thanks are also due to those authors who have sent copies of their books or papers, which are much appreciated.

Grateful acknowledgment is also made to Mrs T. H. Riches for the donation of a collection of books from the library of the late Mr T. H. Riches. These volumes form a very valuable addition to the Library.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the *Journal* of the Association:

Atkins, W. R. G. and Poole, H. H., 1936. The photo-electric measurement of the diurnal and seasonal variations in daylight and a globe integrating photometer. *Phil. Trans. Roy. Soc. Lond.*, A, Vol. ccxxxv, pp. 245–72.

Atkins, W. R. G. and Poole, H. H., 1936. Photo-electric measurements of the luminous efficiency of daylight. *Proc. Roy. Soc. Lond.*, B, Vol. cxxi, pp. 1–17.

Atkins, W. R. G., Poole, H. H. and Stanbury, F. A., 1937. The measurement of the intensity and the colour of the light in woods by means of emission and rectifier photo-electric cells. *Proc. Roy. Soc. Lond.*, B, Vol. cxxi, pp. 427–50.

Bassindale, R., 1936. The developmental stages of three English barnacles: *Balanus balanoides* (Linn.), *Chthamalus stellatus* (Poli) and *Verruca stroemia* (O. F. Müller). *Proc. Zool. Soc.*, pp. 57–74.

Bayliss, L. E., Lythgoe, R. J. and Tansley, K., 1936. Some new forms of visual purple found in sea fishes with a note on the visual cells of origin. *Proc. Roy. Soc. Lond.*, B, Vol. cxx, pp. 95–113.

Berrill, N. J., 1936. Studies in Tunicate development. V. The evolution and classification of Ascidians. *Phil. Trans. Roy. Soc. Lond.*, B, Vol. ccxxvi, pp. 43–70.

Berrill, N. J. and Mees, D. M., 1936. Reorganization and regeneration in *Sabella*. I. Nature of gradient, summation and posterior regeneration. *Journ. Exp. Zool.*, Vol. lxxiii, pp. 67–83.

Berrill, N. J. and Mees, D. M., 1936. Reorganization and regeneration in *Sabella*. II. The influence of temperature. III. The influence of light. *Journ. Exp. Zool.*, Vol. lxxiv, pp. 61–89.

Bogue, J. Y., Chang, I. and Rosenberg, H., 1936. Osmotic pressure and velocity of impulse in *Maia* nerve. *Journ. Physiol.*, Vol. LXXXVII, *Proc. Physiol. Soc.*, pp. 89 *P*–91 *P*.

Bogue, J. Y. and Rosenberg, H., 1936. Excitability of sensory fibres in *Maia* nerve. *Journ. Physiol.*, Vol. LXXXVII, pp. 67–72.

Bogue, J. Y. and Rosenberg, H., 1936. Electrical responses of *Maia* nerve to single repeated stimuli. *Journ. Physiol.*, Vol. LXXXVII, pp. 158–80.

Bogue, J. Y., Rosenberg, H. and Young, J. Z., 1936. Electrotonus in the fin nerve of *Sepia*. *Journ. Physiol.*, Vol. LXXXVI, *Proc. Phys. Soc.*, pp. 6 *P*–7 *P*.

Cohen, A. and Berrill, N. J., 1936. The early development of ascidian eggs. *Biol. Bull.*, Vol. LXX, pp. 78–88.

Cohen, A. and Berrill, N. J., 1936. The development of isolated blastomeres of the ascidian egg. *Journ. Exp. Zool.*, Vol. LXXIV, pp. 91–117.

Cowan, S. L., 1935. The *p*H and CO_2 combining capacity of *Maia* blood. *Journ. Physiol.*, Vol. LXXXIV, *Proc. Phys. Soc.*, pp. 53 *P*–54 *P*.

Day, J. H., 1935. Heterogonic growth in the abdomen of *Carcinus maenas*. *Rept. Dove Mar. Lab.*, Ser. III, No. 3, for Year ending July 31.

Ford, E., 1935. The advance of herring research. *Nature*, Vol. CXXXVI, pp. 896–7.

Fowell, R. R., 1936. Observations on the Sporozoa inhabiting the gut of the Polychaete worm *Polydora flava* Claparède. *Parasitology*, Vol. XXVIII, pp. 414–30.

Grafflin, A. L., 1935. Renal function in marine teleosts. I. Urine flow and urinary chloride. *Biol. Bull.*, Vol. LXIX, pp. 391–402.

Gray, J. and Sand, A., 1936. The locomotory rhythm of the dogfish (*Scyllium canicula*). *Journ. Exp. Biol.*, Vol. XIII, pp. 200–9.

Gray, J. and Sand, A., 1936. Spinal reflexes of the dogfish (*Scyllium canicula*). *Journ. Exp. Biol.*, Vol. XIII, pp. 210–18.

Hogben, L., 1936. The pigmentary effector system. VII. The chromatic function in elasmobranch fishes. *Proc. Roy. Soc. Lond.*, B, Vol. CXX, pp. 142–58.

Howes, N. H., 1936. A study of the histology of the pituitary gland of the skate. *Quart. Journ. Micr. Sci.*, Vol. LXXVIII, pp. 637–51.

Katz, B., 1936. Curarization in the neuro-muscular system of crabs. *Journ. Physiol.*, Vol. LXXXVI, *Proc. Phys. Soc.*, pp. 14 *P*–15 *P*.

Katz, B., 1936. Neuro-muscular transmission in crabs. *Journ. Physiol.*, Vol. LXXXVII, pp. 199–221.

Kitching, J. A., 1936. The physiology of contractile vacuoles. II. The control of body volume in marine Peritricha. *Journ. Exp. Biol.*, Vol. XIII, pp. 11–27.

Lebour, M. V., 1936. Notes on the Plymouth species of *Spirontocaris* (Crustacea). *Proc. Zool. Soc. Lond.*, pp. 89–104.

Lebour, M. V., 1936. Notes on the Plymouth *Processa* (Crustacea). *Proc. Zool. Soc. Lond.*, pp. 609–17.

Löwenstein, O. and Sand, A., 1936. The significance of the spontaneous discharge from the horizontal ampulla of the dogfish. *Journ. Physiol.*, Vol. LXXXVI, *Proc. Phys. Soc.*, pp. 43 *P*–44 *P*.

Löwenstein, O. and Sand, A., 1936. The activity of the horizontal semicircular canal of the dogfish, *Scyllium canicula*. *Journ. Exp. Biol.*, Vol. XIII, pp. 416–28.

Naylor, G. L., 1936. The fucoids of St John's Lake, Plymouth, including a hitherto undescribed form of *Fucus spiralis*. *Revue Algolog.*, pp. 427–39.

Orton, J. H., 1936. Observations and experiments on sex-change in the European oyster. V. A simultaneous study of spawning in 1927 in two distinct geographical localities. *Mém. Mus. Roy. Hist. Nat. Belg.*, Ser. 2, Fasc. 3, pp. 997–1056.

Poole, H. H., 1936. The photo-electric measurement of submarine illumination in off-shore waters. *Proc. Rapp. Verb. Cons. Int.*, Vol. CI, Pt. 2, 12 pp.

Poole, H. H. and Atkins, W. R. G., 1936. The standardization of photo-electric cells for the measurement of energy. *Sci. Proc. Roy. Dublin Soc.*, Vol. xxi, pp. 363–79.

Ramult, M., 1935. Observations on the embryonic larval development in *Sacculina* (Rhizocephala) in changed osmotic conditions of medium. *Bull. Int. Acad. Polon. Sci. Lettres*, B, ii, No. 3–5, pp. 87–109.

Rees, W. J., 1936. The effect of parasitism by larval trematodes on the tissues of *Littorina littorea* (Linné). *Proc. Zool. Soc. Lond.*, pp. 357–68.

Russell, F. S., 1936. A review of some aspects of zooplankton research. *Rapp. Proc. Verb. Cons. Internat.*, Vol. xcv, pp. 3–30.

Russell, F. S., 1936. The importance of certain plankton animals as indicators of water movements in the western end of the English Channel. *Rapp. Proc. Verb. Cons. Internat.*, Vol. c, pp. 7–10.

Russell, F. S., 1936. Submarine illumination in relation to animal life. *Rapp. Proc. Verb. Cons. Internat.*, Vol. ci, Pt. 2, pp. 1–8.

Solandt, D. Y., 1936. The measurement of "accommodation" in nerve. *Proc. Roy. Soc. Lond.*, B, Vol. cxix, pp. 355–79.

Steven, G. A., 1934–5. King Herring. *Trans. Proc. Torquay Nat. Hist. Soc.*, Vol. vii, pp. 31–8.

Tutin, T. G., 1936. New species of *Zostera* from Britain. *Journ. Bot.*, pp. 227–30.

Wilson, D. P., 1936. The development of the Sabellid *Branchiomma vesiculosum*. *Quart. Journ. Micr. Sci.*, Vol. lxxviii, pp. 543–603.

Wilson, D. P., 1935. Under-water photography. *Practical Photography*, iii, pp. 1113–23.

Wilson, D. P., 1936. Larval settlement and the substratum. *The Presidency College Zoology Magazine*, Madras, Vol. iii, pp. 3–7.

Wykes, U. M., 1936. Observations on pigmentary co-ordination in Elasmobranchs. *Journ. Exp. Biol.*, Vol. xiii, pp. 460–6.

Yonge, C. M., 1936. On the nature and permeability of chitin. II. The permeability of the uncalcified chitin lining the foregut of *Homarus*. *Proc. Roy. Soc. Lond.*, B, Vol. cxx, pp. 15–41.

Young, J. Z., 1936. The giant nerve fibres and epistellar body of Cephalopods. *Quart. Journ. Micr. Sci.*, Vol. lxxviii, pp. 367–86.

Young, J. Z., 1936. The innervation and reaction to drugs of the viscera of teleostean fish. *Proc. Roy. Soc. Lond.*, B, Vol. cxx, pp. 303–18.

Membership of the Association.

Governors. During the year the number of Governors was increased to 14 by the election of Dr E. J. Allen as an Honorary Governor.

Founders. The number of Founders remains at 44 of whom 18 are living.

Annual Members. The total number of Annual Members on January 1 1937, was 278, of whom 17 were elected during the year. This is a net increase of 4 over the total of 274 Annual Members on January 1 1936.

Associate Members. The number of Associate Members was reduced from 4 to 3 by the death of Mr Howard Dunn.

Finance.

The Council have again to express their thanks to the Development Commissioners for their continued support to the Plymouth Laboratory. They are grateful also for generous grants from the Fishmongers' Company (£600), the Royal Society (£50), the British Association (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52. 10*s*.), London (£52. 10*s*.), Bristol (£25), Birmingham (£15. 15*s*.), Manchester (£10. 10*s*.), Leeds (£10. 10*s*.), Sheffield (£5. 5*s*.), the Imperial College of Science and Technology (£10), and the Cornwall Sea Fisheries Committee (£10).

Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1937–38:

President

The Lord Moyne, P.C., D.S.O.

Vice-Presidents

The Duke of Bedford, K.G.
The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
Viscount Astor
Lord St Levan, C.B., C.V.O.
The Right Hon. Walter E. Elliot, M.C., M.P., F.R.S.
Lord Noel-Buxton, P.C.
Sir Sidney Harmer, K.B.E., F.R.S.
Sir Nicholas Waterhouse, K.B.E.
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S.
G. A. Boulenger, Esq., F.R.S.
J. O. Borley, Esq., O.B.E.
Col. E. T. Peel, D.S.O., M.C.

COUNCIL

Elected Members

Sir Joseph Barcroft, C.B.E., F.R.S.
M. Burton, Esq.
Prof. H. Graham Cannon, Sc.D., F.R.S.
Capt. G. C. C. Damant, R.N., C.B.E.
H. Muir Evans, Esq., M.D.
Prof. F. E. Fritsch, F.R.S.
Prof. J. Stanley Gardiner, F.R.S.
C. F. A. Pantin, Esq., Sc.D.
E. S. Russell, Esq., O.B.E., D.Sc.
Lieut.-Col. R. B. Seymour Sewell, C.I.E., Sc.D., F.R.S.
J. M. Tabor, Esq.
Prof. W. M. Tattersall, D.Sc.
G. P. Wells, Esq.
Prof. C. M. Yonge, D.Sc.
J. Z. Young, Esq.

Chairman of Council

Prof. E. W. MacBride, D.Sc., F.R.S.

Hon. Treasurer

Guy Wood, Esq., M.B., M.R.C.P., The Charterhouse, London, E.C. 1

Secretary

Stanley Kemp, Esq., Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. Bidder, Esq., Sc.D.
E. T. Browne, Esq.
The Lord Moyne, P.C., D.S.O.
H. G. Maurice, Esq., C.B. (Ministry of Agriculture and Fisheries)
Sir Vincent Baddeley, K.C.B. (Prime Warden of the Fishmongers' Company)
Guy Wood, Esq., M.B., M.R.C.P. (Fishmongers' Company)
R. L. Newman, Esq. (Fishmongers' Company)
Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University)
J. Gray, Esq., M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association)
Prof. E. W. MacBride, D.Sc., F.R.S. (Zoological Society)
Sir Sidney Harmer, K.B.E., F.R.S. (Royal Society)
E. J. Allen, Esq., C.B.E., D.Sc., F.R.S. (*Honorary*)

LIST OF ANNUAL SUBSCRIPTIONS

Paid during the Year, April 1 1936 to March 31 1937

	£	s.	d.
E. J. Allen, Esq., C.B.E., D.SC., F.R.S.	1	1	0
Aquario Vasco da Gama	1	1	0
Miss D. Atkins	1	1	0
W. H. Atkinson, Esq.	1	1	0
E. Baldwin, Esq. (1936 and 1937)	2	2	0
Prof. Sir Joseph Barcroft, F.R.S.	1	1	0
Miss M. G. Barnes	1	1	0
W. H. Barrett, Esq.	1	1	0
Dr J. B. Bateman	1	1	0
L. C. Beadle, Esq.	1	1	0
R. L. A. Beauchamp, Esq.	1	1	0
G. R. de Beer, Esq.	1	1	0
Miss C. R. Begg (1937 and 1938)	2	2	0
J. Bělehrádek, Esq., M.D.	1	1	0
D. M. Bickmore, Esq.	1	1	0
Birkbeck College	1	1	0
W. Birtwistle, Esq.	1	1	0
H. H. Bloomer, Esq.	1	1	0
H. Moss Blundell, Esq., C.B.E.	1	1	0
Mrs H. Moss Blundell	1	1	0
Dr B. G. Bogorov	1	1	0
Dr J. Yule Bogue (1936 and 1937)	2	2	0
Capt. R. J. B. Bolitho	1	1	0
J. R. Bolton, Esq.	1	1	0
Dr J. Borowik	1	1	0
L. A. Borradaile, Esq., SC.D.	1	1	0
S. J. A. Bosanquet, Esq.	1	1	0
Prof. C. L. Boulenger	1	1	0
E. G. Boulenger, Esq. (1935 and 1936)	2	2	0
Col. Sir Henry Bowles, Bart.	1	1	0
A. Bowman, Esq., D.SC.	1	1	0
Prof. A. E. Boycott, F.R.S.	1	1	0
Brighton Public Library	1	1	0
L. R. Brightwell, Esq.	1	1	0
Bristol University	1	1	0
Miss E. M. Brown	1	1	0
H. H. Brown, Esq. (1936 and 1937)	2	2	0
Dr H. O. Bull	1	1	0
W. S. Bullough, Esq.	1	1	0
R. H. Burne, Esq., F.R.S.	1	1	0
M. Burton, Esq.	1	1	0
L. W. Byrne, Esq.	1	1	0
Prof. H. Graham Cannon, SC.D., F.R.S.	1	1	0
J. N. Carruthers, Esq., D.SC.	1	1	0
Dr G. S. Carter	1	1	0
Paymaster-Capt. R. Charles, R.N. (retd.)	1	1	0
Charterhouse School	1	1	0
R. G. Church, Esq.	1	1	0
R. S. Clark, Esq., D.SC. (1936 and 1937)	2	2	6
P. T. Clothier, Esq. (1937 and 1938)	2	2	0
Coastguard and Fisheries Service, Alexandria	1	1	0
Prof. F. J. Cole, D.SC., F.R.S.	1	1	0
H. A. Cole, Esq.	1	1	0
J. S. Colman, Esq.	1	1	0
Col. R. Stapleton Cotton	1	1	0
G. I. Crawford, Esq.	1	1	0
L. R. Crawshay, Esq.	1	1	0
P. R. Crimp, Esq.	1	1	0
Miss D. R. Crofts	1	1	0
N. Cuthbertson, Esq. (1936 and 1937)	2	2	0
S. B. Davie, Esq.	1	1	0
F. M. Davis, Esq.	1	1	0
Ben Dawes, Esq., D.SC.	1	1	0
Department of Fisheries, Bangkok (1936 and 1937)	2	2	0
Division of Fisheries, Capetown	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
F. M. Duncan, Esq. (1935 and 1936)	2	2	0
F. M. Dyke, Esq.	1	1	0
Miss N. B. Eales, D.SC.	1	1	0
Prof. L. E. S. Eastham	1	1	0
P. Eggleton, Esq., D.SC.	1	1	0
The Rt. Hon. Walter E. Elliot, M.C., M.P.	1	1	0
C. E. D. Enoch, Esq.	1	1	0
H. Muir Evans, Esq., M.D.	1	1	0
G. P. Farran, Esq.	1	1	0
Dr Hussein Faouzi (1933, 1934 and 1935)	3	3	0
Miss R. Fellowes	1	1	0
Prof. R. A. Fisher, SC.D., F.R.S.	1	1	0
Miss K. M. G. Fleming	1	1	0
E. Ford, Esq.	1	1	0
E. B. Ford, Esq.	1	1	0
Dr G. H. Fowler	1	1	0
C. L. Fox, Esq.	1	1	0
Dr E. L. Fox	1	1	0
Prof. H. Munro Fox, F.R.S.	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
F. C. Fraser, Esq.	1	1	0
Prof. F. E. Fritsch, F.R.S.	1	1	0
Major A. Gardner, M.C.	1	1	0
H. C. Gilson, Esq.	1	1	0
Prof. E. S. Goodrich, D.SC., F.R.S.	1	1	0
Alastair Graham, Esq.	1	1	0
Michael Graham, Esq.	1	1	0
Ronald Grant, Esq. (1936 and 1937)	2	2	0
Dr A. M. H. Gray	1	1	0
Prof. J. Gray, M.C., SC.D., F.R.S.	1	1	0

	£	s.	d.
H. P. Hacker, Esq., M.D., D.SC.	1	1	0
Wilfred Hall, Esq. (1934, 1935 and 1936)	3	3	0
I. I. Hamilton, Esq. (1935, 1936 1937)	3	3	0
Prof. A. C. Hardy	1	1	0
Prof. C. R. Harington, F.R.S.	1	1	0
T. J. Hart, Esq.	1	1	0
P. H. T. Hartley, Esq.	1	1	0
H. W. Harvey, Esq., SC.D. (1935, 1936 and 1937)	3	3	0
Prof. L. A. Harvey	1	1	0
G. T. D. Henderson, Esq., D.SC.	1	1	0
C. C. Hentschel, Esq.	1	1	0
C. F. Hickling, Esq.	1	1	0
Prof. Sydney J. Hickson, D.SC., F.R.S.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
M. A. C. Hinton, Esq.	1	1	0
Prof. K. Hirasaka (1935 and 1936)	2	2	0
Prof. L. T. Hogben, Esq., D.SC. (1935 and 1936)	2	2	0
Dr E. G. Holmes (1935 and 1936)	2	2	0
F. R. Horne, Esq.	1	1	0
H. D. Howell, Esq.	1	1	0
N. H. Howes, Esq.	1	1	0
A. A. Hudson, Esq.	1	1	0
O. D. Hunt, Esq.	1	1	0
Prof. J. S. Huxley	1	1	0
Miss P. M. Jenkin	1	1	0
Miss M. Jepps	1	1	0
D. D. John, Esq.	1	1	0
Rodney R. M. Jones, Esq.	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., SC.D., F.R.S.	1	1	0
Mrs A. Redman King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
Dr J. A. Kitching	1	1	0
Dr G. Lapage	1	1	0
Prof. R. D. Laurie	1	1	0
D. W. le Mare, Esq.	1	1	0
A. G. Lowndes, Esq.	1	1	0
C. Lucas, Esq.	1	1	0
Adrian Lumley, Esq.	1	1	0
Prof. E. W. MacBride, D.SC., F.R.S.	1	1	0
Lt.-Col. W. Mackenzie, O.B.E.	1	1	0
Prof. D. L. Mackinnon, D.SC.	1	1	0
G. I. Mann, Esq.	1	1	0
Prof. B. J. Marples	1	1	0
Sir John D. Marsden, Bart., J.P.	1	1	0
Capt. W. N. McClean	1	1	0
C. R. McKenzie, Esq.	1	1	0
Milford Haven Trawler Owners' Association Ltd.	1	1	0
W. S. Millard, Esq.	1	1	0
Sir Peter Chalmers Mitchell, Kt., C.B.E., F.R.S.	1	1	0
Mrs E. M. Morehouse	1	1	0
C. C. Morley, Esq.	1	1	0
Mount Desert Island Biological Laboratory (1935 and 1936)	2	2	0
Dr J. Mukerji	1	1	0

	£	s.	d.
National Museum of Wales	1	1	0
Morley H. Neale, Esq.	1	1	0
Messrs Neale and West Ltd.	1	1	0
H. G. Newth, Esq. (1931, 1932, 1933, 1934 and 1935)	5	0	0
Dr A. G. Nicholls	1	1	0
J. A. Nicholson, Esq.	1	1	0
J. R. Norman, Esq.	1	1	0
Dr C. L. Oakley	1	1	0
Office Scientifique et Technique des Pêches Maritimes, Port de l'Orient Keroman	1	1	0
Charles Oldham	1	1	0
G. W. Olive, Esq.	1	1	0
Prof. J. H. Orton, D.SC.	1	1	0
R. Palmer, Esq.	1	1	0
C. W. Parsons, Esq.	1	1	0
Major J. S. Paterson (1936 and 1937)	1	19	6
W. N. Paton, Esq.	1	1	0
Messrs Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs Peacock and Buchan, Ltd.	1	1	0
Pease Laboratories Incorporated	1	1	0
Colonel E. T. Peel, D.S.O., M.C.	1	1	0
F. T. K. Pentelow, Esq.	1	1	0
Prof. E. Percival	1	1	0
F. Perkins, Esq.	1	1	0
L. E. R. Picken, Esq.	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Educational Authority	1	1	0
Plymouth Proprietary Library	1	1	0
Plymouth Public Library	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
Portsmouth Municipal College	1	1	0
W. Procter, Esq.	1	1	0
Queen Mary College	1	1	0
Dr H. E. Quick, F.R.C.S.	1	1	0
Dr A. Ramalho	1	1	0
G. Rayner, Esq. (1935, 1936 and 1937)	3	3	0
H. C. Regnart, Esq.	1	1	0
D. M. Reid, Esq.	1	1	6
Prof. L. W. P. Renouf	1	1	0
Lord Rothschild	1	1	0
E. S. Russell, Esq., D.SC.	1	1	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Capt. the Hon. Lionel St Aubyn, M.V.O.	1	1	0
The Rt Hon. Lord St Levan, C.B., C.V.O.	1	1	0
Dr A. Sand	1	1	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq.	1	1	0
Dr F. F. Schacht (the late)	1	1	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S.	1	1	0
Miss Lilian Sheldon	1	1	0

	£	s.	d.
C. J. Shen, Esq.	1	1	0
Prof. W. Rae Sheriffs, D.Sc.	1	1	0
H. P. Sherwood, Esq.	1	1	0
B. Webster Smith, Esq.	1	1	0
F. G. W. Smith, Esq.	1	1	0
J. E. Smith, Esq.	1	1	0
V. D. Van Someren, Esq.	1	1	0
Prof. E. A. Spaul (1936 and 1937)	2	2	0
G. M. Spooner, Esq.	1	1	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	3
Prof. T. A. Stephenson, D.Sc.	1	0	0
Mrs G. A. Steven	1	1	0
C. Stewart-Evison, Esq.	1	1	0
H. G. Stubbings, Esq. (1937 and 1938)	2	2	0
Mrs R. S. Sturdy	1	1	0
E. J. Tabor, Esq.	1	1	0
H. E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W. M. Tattersall, D.Sc.	1	1	0
Prof. G. I. Taylor, F.R.S.	1	1	0
Sir Charles Howell Thomas, K.C.B., C.M.G.	1	1	0
Sir Herbert Thompson, Bart.	1	1	0
Torquay Natural History Society	1	1	0
Miss E. M. Tregoning (1937 and 1938)	2	2	0
P. H. Truelove, Esq.	1	1	0
P. Ullyott, Esq.	1	1	0
Prof. S. L. Vella	1	1	0
H. M. Vickers, Esq.	1	1	0
Dr A. Walton	1	1	0
Sir Nicholas E. Waterhouse, K.B.E.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
G. Weaver, Esq.	1	1	0
Mrs F. J. Weldon (the late)	1	1	0
A. E. J. Went, Esq. (1936 and 1937)	2	2	0
Miss K. M. White	1	1	0
D. P. Wilson, Esq.	1	1	0
Mrs D. P. Wilson, Ph.D.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq., F.R.G.S.	1	1	0
V. C. Wynne-Edwards, Esq.	1	1	0
Prof. C. M. Yonge, D.Sc.	1	1	0
John Z. Young, Esq.	1	1	0
	£294	13	9

DONATION TO THE GENERAL FUND

For the year April 1 1936 to March 31 1937

	£	s.	d.
Cuprinol Ltd.	5	5	0
	£5	5	0

THE MARINE BIOLOGICAL ASSOCIATION

INCOME AND EXPENDITURE ACCOUNT

	£	s.	d.	£	s.	d.
To Salaries, including Institution's Contributions to Superannuation				7,829	19	10
,, Laboratory Wages, including National Insurance and Institution's Contributions to Superannuation ...				2,235	11	6
,, Depreciation of Library				471	9	4
,, Scientific Publications, *Less* Sales and Grant... ...				603	3	8
,, Upkeep of Laboratories and Tank Rooms:						
Buildings and Machinery	557	19	7			
Electricity, Gas, Coal, Oil and Water	325	15	2			
Chemicals and Apparatus	362	18	11			
Rates, Taxes and Insurance	113	15	5			
Travelling Expenses	86	5	3			
Stationery, Postages, Telephone, Carriage and Sundries	348	6	9			
Specimens	105	15	0			
				1,900	16	1
,, Maintenance and Hire of Boats:						
Wages, including Diet Allowance, National Insurance and Casual Labour	1,686	12	9			
Coal, Water, Oil, Petrol, etc.	273	5	1			
Maintenance and Repairs with Nets, Gear and Apparatus	927	10	2			
Purchase of Material for Nets for Sale, excluding Labour	170	12	1			
Boat Hire and Collecting Expenses	33	18	5			
Insurance	281	7	4			
				3,373	5	10
,, Transfer to Depreciation Reserve Account				284	10	2
				£16,698	16	5

OF THE UNITED KINGDOM

YEAR ENDED MARCH 31 1937

	£	s.	d.	£	s.	d.
By Grants						
Ministry of Agriculture and Fisheries Grant from Development Fund	12,485	10	0			
Fishmongers' Company	600	0	0			
British Association	50	0	0			
Royal Society	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	10	0	0			
				13,225	10	0
,, Subscriptions (excluding Subscriptions received in advance)...				277	2	0
,, Donations				5	5	0
,, Sales:						
Specimens	1,222	0	8			
Fish (*less* Expenses)	77	0	10			
Nets, Gear and Hydrographical Apparatus	317	12	6			
				1,616	14	0
,, Table Rents (including University of Cambridge £105; Oxford £52. 10*s*.; London £52. 10*s*.; Bristol £25; Birmingham £15. 15*s*.; Manchester £10. 10*s*.; Sheffield £5. 5*s*.; Imperial College £10; Trustees of Ray Lankester Fund £20)				467	12	6
,, Tank Room Receipts				593	7	6
,, Interest on Investments, less Tax:						
General Fund	14	6	11			
Depreciation Fund	34	10	7			
Composition Fee Fund	2	18	0			
				51	15	6
,, Interest on Bank Deposit Account (*less* Bank Charges)				2	12	9
,, Sale of Dr M. V. Lebour's Book				1	18	8
,, Sale of "Marine Fauna of Plymouth"				7	1	6
,, Income Tax Recoverable				16	0	4
,, Balance being Deficiency for the Year				433	16	8
				£16,698	16	5

THE MARINE BIOLOGICAL ASSOCIATION

BALANCE SHEET

		£ s. d.	£ s. d.
SUNDRY CREDITORS:			
On Open Account			386 4 6
PROPORTION OF SUBSCRIPTIONS RECEIVED IN ADVANCE ...			129 3 0
JEWISH SCHOLARSHIP FUND:			
As at March 31 1936		67 12 4	
Add: Fourth Instalment received		100 0 0	
		167 12 4	
Less: Expenditure		166 17 6	
			14 10
E. T. BROWNE—SCHOLARSHIP GRANT FUND:			
As at March 31 1936		330 5 0	
Interest on Bank Deposit		1 5 7	
		331 10 7	
Less: Expenditure		199 2 3	
			132 8 4
AQUARIUM GUIDE PRINTING FUND:			
As at March 31 1936		7 1 0	
Sale of Aquarium Guides		14 9 0	
		21 10 0	
Less: Expenditure		1 10 0	
			20 0 0
Dr H. B. MOORE—SPECIAL GRANT FUND:			
Grant received		300 0 0	
Less: Expenditure		300 0 0	
			– – –
T. G. TUTIN—SPECIAL GRANT FUND:			
As at March 31 1936		10 8 4	
Grant received		62 10 0	
		72 18 4	
Less: Expenditure		72 18 4	
			– – –
MACKEREL RESEARCH FUND:			
Grant received		488 6 9	
Less: Expenditure		431 14 10	
			56 11 11
RESERVE FOR DEPRECIATION OF BOATS AND MACHINERY:			
As at March 31 1936		1,459 16 5	
Add: Transfer from Income and Expenditure Account ...		284 10 2	
			1,744 6 7
COMPOSITION FEE FUND:			
As at March 31 1936			126 0 0
SURPLUS:			
As at March 31 1936		6,505 16 5	
Deduct: Deficiency for the year	433 16 8		
Less: Profit on Sale of New Zealand Stock	80 16 6		
		353 0 2	
			6,152 16 3
			£8,748 5 5

W. M. TATTERSALL }
G. P. WELLS } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the expenditure on erection of Buildings on Land held on Lease from the War Department is up so as to exhibit a true and correct view of the state of the Association's affairs, according the Association.

34 *and* 35 *Bedford Street,*
Plymouth. April 17 1937.

OF THE UNITED KINGDOM

MARCH 31 1937

	£	s.	d.	£	s.	d.
Boats and Equipment, as per Valuation as estimated by the Director at March 31 1931						
S.S. *Salpa*	2,000	0	0			
Motor Boat	150	0	0			
Nets, Gear and General Equipment	27	0	0	2,177	0	0
Laboratory Apparatus, Engines and Pumps:						
As per Valuation as estimated by the Director at March 31 1931, plus additions at Cost						
As at March 31 1936	831	7	5			
Additions during the year (Net)...	191	15	0	1,023	2	5
Library:						
As per Valuation as estimated by the Director at March 31 1931, plus additions at Cost, *less* Depreciation						
As at March 31 1936	2,257	1	4			
Additions during the year	491	10	4			
	2,748	11	8			
Less: Depreciation	471	9	4	2,277	2	4
Stock of Specimens, Chemicals and Journals:						
As estimated by the Director				375	0	0
Sundry Debtors:						
Sale of Specimens, Journals, Nets, Gear and Apparatus	199	8	4			
Table Rent	5	5	0	204	13	4
Income Tax Recoverable				21	18	11
Prepayments				122	6	1
General Fund Investment at Market Value as at March 31 1931:						
£352. 2*s*. 3*d*. Local Loans 3 % ... ... (Market value at date £310. 4*s*.)				232	7	10
Depreciation Fund Investment at Cost:						
£590. 6*s*. Local Loans 3 %	506	10	9			
£1216. 7*s*. 5*d*. Conversion Loan 3 %	1,237	15	10			
(Market value at date £1741. 1*s*. 4*d*.)				1,744	6	7
Composition Fund Investments at Cost:						
£18. 8*s*. 6*d*. Local Loans 3 %	15	15	0			
£108. 6*s*. 5*d*. Conversion Loan 3 %	110	5	0			
(Market value at date £125. 4*s*.)				126	0	0
Cash at Bank and in Hand:						
Coutts and Co.—Current Account	2	18	3			
” Deposit Account	125	0	0			
Lloyds Bank Limited	250	15	8			
Cash in Hand	65	14	0	444	7	11
				£8,748	5	5

Association and have obtained all the information and explanations we have required. Capital excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn to the best of our information and the explanations given to us and as shown by the books of

Price, Waterhouse and Co.

Edward G. Browne

Edward Thomas Browne

1866–1937

Members of the Association, especially those who have served on the Council and many biologists who have worked at the Plymouth Laboratory during the last forty years, will have learned with sorrow and regret of the death of Edward Thomas Browne of "Anglefield", Berkhamsted, on December 10, 1937, in his 72nd year, following a short illness. As a student at Queen's College, Oxford, Browne did not read biology, but after graduation spent some years in London, where he developed an interest in microscopy and the study of freshwater pond life. He became a Fellow of the Royal Microscopical Society in 1884 and a member of the Quekett Club in 1887, and was an active worker with both these societies, serving for a time on the council of each and maintaining his interest in them throughout his life.

During the session 1891–92 Browne attended a full course of lectures and practical work in Zoology under Prof. W. F. R. Weldon at University College, London. In the autumn of 1892 he began investigations on coelenterates in the old research laboratory which had been arranged by Ray Lankester on the north side of the gallery surrounding the Zoological Lecture Theatre. In this narrow space tables were provided for six research workers, and it was here that I first met Browne. The rest of the party consisted of H. F. Thompson (now Sir Herbert Thompson), the late Miss Florence Buchanan, then working at marine Polychaetes but who subsequently did Physiological research with Burdon-Sanderson in Oxford, Miss Kircaldy of Oxford and Miss Margaret Robinson, a former Newnham student, who seventeen years later became Browne's wife. In addition to Prof. Weldon, who was full of enthusiasm for the Plymouth Laboratory and its work, Dr G. Herbert Fowler, Assistant Professor in the Department, and at the time Secretary of the Marine Biological Association, did much to encourage and help us all and to direct our attention to problems of marine animal life.

In the spring of 1893 Browne spent a month at the Marine Station at Port Erin, in the Isle of Man, and in September paid his first visit to the Plymouth Laboratory. A similar programme was followed in 1894, the intermediate months being spent at University College. In the spring of 1895 he went with W. I. Beaumont and F. W. Gamble to Valencia, on the south-west coast of Ireland, and also spent a month at Plymouth in the summer. In the following year a larger party was organized by him to carry out investigations at Valencia, the additional members being Prof. F. E. Weiss, A. O. Walker and M. D. Hill. The party received much help from the Misses Delap, who had previously taken great interest in the fauna of Valencia Harbour, and from them in later

SEP 1954
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

years Browne received constant supplies of new material with notes on observations made on the living organisms.

By this time Browne had settled down to specialize on the Medusae and Hydroids, and after the publication of his two papers in the *Proceedings of the Zoological Society of London* in 1896 and 1897 he was quickly recognized as a leading authority on these coelenterates. For many years he continued to work at University College during the winter half of the year, attending with great regularity from day to day. Already in 1896 and 1897 he was planning a monograph on the British Medusae, using every endeavour to follow their full life-histories and to connect them with their proper hydroids. As the illustrations to his published papers show he was a skilful artist. Many plates were prepared for use in the proposed monograph, and detailed notes were written. When, two or three years ago, he felt that he would not himself be able to complete the work, he arranged with Mr F. S. Russell to carry on the scheme, paying for a trained biological assistant to help him in the task. He has made provision also for the publication of the monograph when ready under their joint names, so that there is every hope that this part of his life work will not be lost.

In connexion with this work Browne continued to visit different marine laboratories, and made expeditions to places specially suitable for collecting the material he required. His visits to the Plymouth Laboratory as a worker continued from time to time during the next 15 or 20 years, and special mention should be made of the two papers "On keeping medusae alive in an aquarium" (1898) and "A new method for growing hydroids in small aquaria by means of a continuous current tube" (1907). In the first of these he emphasized the advantages of keeping small pelagic marine animals in constant movement by mechanical means in order to keep them healthy in an aquarium. For this purpose he designed an apparatus known as the "plunger-jar", which is still much used at Plymouth, as well as in other biological laboratories. Both this and the "continuous current tube" illustrate one side of his ability, the successful designing and handling of instruments and apparatus for the purposes of his research. His whole technique was excellent and he paid the greatest attention to detail and scientific accuracy. His early experience as a microscopist no doubt served him in good stead in his later work.

Special mention should be made of Browne's work with Rupert Vallentin, which belongs to this period. A series of papers on the Fauna of Falmouth Harbour was published in the *Report of the Royal Cornwall Polytechnic Society* and in the *Journal of the Royal Institution of Cornwall* between 1891 and 1897 (see 1899, p. 691 in list of works below), by Vallentin, which are liable to be lost sight of. Browne visited him and collected with him in Falmouth and they also spent some time together in the Scilly Islands (1904). Vallentin, who had studied Zoology in Munich under Richard Hertwig, visited the Falkland Islands in 1898–99, bringing back a fine collection of Medusae which he handed over to Browne. A preliminary report on these was published in 1902, and a manuscript with drawings for the full report was prepared but not published. This will probably be revised and arranged for publication by Dr P. L. Kramp of Copenhagen.

On his marriage in December 1909 to Miss M. Robinson, his colleague for many years in the research laboratory at University College, London, he made his home at "Anglefield", Berkhamsted, a house with a good garden on the outskirts of the town. Here he built a special laboratory for his work, and for the housing of his numerous collections and the fine special library on coelenterates which he had got together. Remarkably characteristic was the careful way in which the collections were preserved and arranged, and both these and the scientific pamphlets card-indexed, so that anything could be found at a moment's notice. He had also accumulated a great mass of typewritten notes, all arranged with equal care.

Owing to the reputation he had made as a specialist on the medusae, and the care and accuracy of his work, he at this time received numerous requests to report on collections of medusae from all parts of the world. Although the examination of these collections and the preparation of the reports on them interfered with the progress of the monograph on British medusae, he felt the work well worth undertaking, giving him as it certainly did a broader grasp of the group as a whole, and he hoped that the British monograph would gain greatly in the end by the delay. When therefore he was settled in his own laboratory at "Anglefield", he worked chiefly on foreign collections, and the reports he published, all of which are illustrated by his own beautiful and accurate figures, show that he put much time and effort into making them as perfect as the specimens allowed.

He was fortunate when he first went to Berkhamsted in having as a near neighbour the Rev. Canon A. M. Norman, in whom he found a marine naturalist after his own heart. The two became very close friends, for in addition to this bond, Browne and Norman were both keen gardeners and both found the care of their gardens a relief from the close work of systematic zoology. Norman's death was a great grief to Browne.

He became a Fellow of the Zoological Society in 1894, and when he was at University College he paid frequent visits to the Zoological Gardens. Among his other activities he was a good photographer and spent much time and effort in getting fine pictures of many of the animals in the Gardens in characteristic attitudes, and especially the birds.

After his marriage and settlement at "Anglefield", Browne, who was a good business man, took a special interest in the administration of several of the scientific societies of which he was a member. He was elected a Fellow of the Linnean Society in 1913 and served on the Council from 1915 to 1923, being a Vice-President from 1920 to 1923. He took great interest in the work of the Council, and was especially active as a member of the Library Committee.

He was also a member of the Challenger Society for the Promotion of Oceanography and a regular attendant at its meetings.

But I think we can claim that he gave his most active support to the Marine Biological Association and its Plymouth Laboratory. He became a member of the Association in 1893, the year in which he first visited the Laboratory, and from 1895 onwards he was always active and helpful in advising on business and administrative matters. He served as an ordinary member of Council from 1913 until 1919, in which year he supported his friend Dr G. P. Bidder, who was collecting a fund for the enlargement of the Laboratory buildings, by giving a donation of £500 which made the proposed scheme possible. By this donation he became a Life-Governor with a permanent seat on the Council of the Association. He gave substantial financial help to all subsequent efforts for the enlargement of the Laboratory and the extension of its work, spending also much time and thought on the various plans proposed. In all such matters his advice and business experience contributed greatly to the progress of the Association's work. His special donations made during his lifetime amounted to £2655, and in addition he provided funds to enable young naturalists to carry out particular lines of work in the Laboratory. Substantial sums have also been left to the Association in his will to enable these activities to continue.

Browne was a real "naturalist", in the old sense in which that word was understood, who, as a result of an academic training, early took a useful part in the transition that led to the "ecologists" of to-day. His interest was primarily in living animals and plants in their natural surroundings and for him work in the laboratory was undertaken as an aid to elucidating the relationships of the organism to the physical and biological conditions in which it lived. His interests were not confined to his hydroids and medusae, but extended to all the animals of the sea and equally to the birds and plants of the countryside and the garden.

As a man he was generous and good-hearted, the staunch friend of a large and varied group of biologists, whom he was always anxious to help in any way he could in their scientific work. His knowledge and experience were freely given to them all and especially he found great pleasure in helping those just entering on biological research. But it was not until one had the happiness to know him in his own charming home, with a wife who sympathized so fully with all his pursuits, that the full measure of his kindness was made plain.

E. J. ALLEN.

LIST OF PAPERS BY E. T. BROWNE

1895. Report on the medusae of the L.M.B.C. District. *Trans. Lpool Biol. Soc.*, Vol. IX, pp. 243–86.

—— On the variation of the tentaculocysts of *Aurelia aurita*. *Quart. Journ. Micr. Sci.*, Vol. XXXVII, pp. 245–51.

—— On the variation of *Haliclystus octoradiatus*. *Quart. Journ. Micr. Sci.*, Vol. XXXVIII, pp. 1–8.

1896. On British hydroids and medusae. *Proc. Zool. Soc. London*, pp. 459–500.

—— On the changes in the pelagic fauna of Plymouth during September, 1893 and 1895. *Journ. Mar. Biol. Assoc.*, Vol. IV, pp. 168–73.

—— The medusae of Valencia Harbour, County Kerry. *Irish Naturalist*, July, pp. 179–81.

1897. On *Tubularia crocea* in Plymouth Sound. *Journ. Mar. Biol. Assoc.*, Vol. V, pp. 54–5.

—— The hydroids of Valencia Harbour, Ireland. *Irish Naturalist*, pp. 241–6.

—— On British medusae. *Proc. Zool. Soc. London*, pp. 816–35.

—— Revised list of hydromedusae of L.M.B.C. District. *Trans. Lpool Biol. Soc.*, Vol. XI, pp. 147–50.

1898. On keeping medusae alive in an aquarium. *Journ. Mar. Biol. Assoc.*, Vol. V, pp. 176–80.

—— On the pelagic fauna of Plymouth for September, 1897. *Journ. Mar. Biol. Assoc.*, Vol. V, pp. 186–92.

1899. (With Beaumont, W. I. and Gamble, F. W.) The fauna and flora of Valencia Harbour on the west coast of Ireland. I. The pelagic fauna (1895–98). II. The medusae (1895–98). *Proc. R. Irish Acad.*, Ser. 3, Vol. V, pp. 667–93, 694–736.

1901. Variation in *Aurelia aurita*. *Journ. Biometrika*, Vol. I, pp. 90–108.

1902. A preliminary report on hydromedusae from the Falkland Islands. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. IX, pp. 272–84.

1903. Report on some medusae from Norway and Spitzbergen. *Bergens Mus. Aårbog*, No. 4, pp. 1–36.

1904. (With Vallentin, R.) On the marine fauna of the Isles of Scilly. *Journ. Roy. Inst. Cornwall*, Vol. L, pp. 120–32.

—— Hydromedusae, with a revision of the Williadae and Petasidae. *Faun. Geogr. Maldive Laccadive Archip.*, Vol. II, pp. 722–49.

—— Scyphomedusae. *Faun. Geogr. Maldive Laccadive Archip.*, Vol. II, Supp. pp. 958–72.

1905. A report on the medusae found in the Firth of Clyde (1901–2). *Proc. Roy. Soc. Edin.*, Vol. XXV, pp. 738–78.

—— Notes on the pelagic fauna of the Firth of Clyde (1901–2). *Proc. Roy. Soc. Edin.*, Vol. XXV, pp. 779–91.

1905 Report on the medusae (Hydromedusae, Scyphomedusae, Ctenophora) collected by Professor Herdman at Ceylon, in 1902. *Report on the Pearl Oyster Fisheries of the Gulf of Manaar Royal Soc. Suppl. Rep.*, Vol. XXVII, pp. 131–66.

1906. On the fresh-water medusa *Limnocnida tanganicae* and its occurrence in the River Niger. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XVII, pp. 305–6.

—— On the fresh-water medusa liberated by *Microhydra ryderi*, Potts, and a comparison with *Limnocodium*. *Quart. Journ. Micr. Sci.*, Vol. L, pp. 635–45.

—— Biscayan plankton collected during a cruise of H.M.S. *Research* 1900. Pt IX. The medusae. *Trans. Linn. Soc., 2nd Ser. Zool.*, Vol. X, pp. 163–187.

1907. A new method for growing hydroids in small aquaria by means of a continuous current tube. *Journ. Mar. Biol. Assoc.*, Vol. VIII, pp. 37–43.

—— The hydroids collected by the *Huxley* from the north side of the Bay of Biscay in August, 1906. *Journ. Mar. Biol. Assoc.*, Vol. VIII, pp. 15–36.

—— A revision of the medusae belonging to the family Laodiceidae. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. XX, pp. 457–80.

1908. The medusae of the Scottish National Antarctic Expedition. *Trans. Roy. Soc. Edin.*, Vol. XLVI, pp. 233–51.

—— On the fresh-water medusa, *Limnocnida tanganicae*, discovered in the River Niger by the late J. S. Budgett. *Budgett Memorial Volume*, pp. 471–80.

1910. Coelenterata. V. Medusae. *Nat. Antarct. Exped., Nat. Hist.*, Vol. V, pp. 1–62.

1912. "The floating animals" and "Preservation of marine organisms." (With G. H. Fowler and E. J. Allen.) *Science of the Sea*. Prepared by the Challenger Society and edited by G. Herbert Fowler. London, Murray. 1912. Chapters V and XI, pp. 162–99 and 344–82. Second edition (revised). Oxford: Clarendon Press. 1928. pp. 206–40 and 386–425.

1916. Medusae from the Indian Ocean. (Collected by Prof. Stanley Gardiner in H.M.S. *Sealark*, in 1905.) *Trans. Linn. Soc., 2nd Ser. Zool.*, Vol. XVII, pp. 169–210.

—— Notes on some jelly-fishes from Okhamandal in Kattiawar collected by Mr James Hornell in 1904–5. *Rep. Govt. Baroda on Mar. Zool. Okhamandal in Kattiawar*, Pt. II, pp. 151–5.

1919–20. Ernst Heinrich Philipp August Haeckel. *Proc. Linn. Soc.*, Sess. 132, pp. 39–43.

1926. Siphonophorae from the Indian Ocean collected by Prof. Stanley Gardiner in H.M.S. *Sealark*. *Trans. Linn. Soc., 2nd Ser. Zool.*, Vol. XIX, pp. 55–86.

—— Report on the medusae, Cambridge Expedition to the Suez Canal. *Trans. Zool. Soc.*, London, Vol. XXII, pp. 105–15.

THE PLYMOUTH OFFSHORE MEDUSA FAUNA

By F. S. Russell, B.A., F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–5)

CONTENTS

	PAGE
Introduction	411
The Plymouth Medusa Fauna	412
The Ringtrawl Catches, 1930–7	418
Observations on Certain Medusae	420
Purena gemmifera (Forbes)	420
Zanclea costata Gegenbaur	420
Bougainvillia britannica Forbes	421
Bougainvillia principis (Steenstrup)	423
Turritopsis nutricula McCrady	423
Amphinema rugosum Mayer	423
Pochella polynema Hartlaub	425
Laodicea undulata (Forbes & Goodsir)	427
Cosmetira pilosella Forbes	428
Tiaropsis multicirrata (M. Sars)	429
Phialidium hemisphericum (L.)	429
Eucheilota clausa (Hincks)	432
Helgicirrha schulzei Hartlaub	432
Aglantha rosea (Forbes)	433
Summary	435
References	438

Introduction

A system of regular weekly collecting with the 2 m. stramin ringtrawl was started in 1930 with the object of comparing fluctuations in the composition of the plankton over a number of years, in the hope that certain animals might thus be found which could be used as "an index of conditions that may lead to other fluctuations such as those of the fisheries" (Russell, 1933). A direct outcome of this work has been the recognition of a number of animals that can be used as indicators of water masses and the correlation of variations in their occurrence with the numbers of young fish in the plankton. In the preliminary paper quoted above it was noted that such changes as occurred in the composition of the plankton from year to year were especially noticeable in the medusa population. Medusae have been regarded by some workers (e.g. Kramp, 1927) as very valuable indicators, liberated at certain times from their hydroids in fixed localities and drifting in the water masses for periods that can be estimated with a correct knowledge of their life histories. Since the inception of this work in 1930 close attention has been paid to certain medusae which appeared to be spasmodic in their occurrence. But it was soon noticed that the differences between some years were so marked that it was advisable to distinguish all medusae occurring in the catches. The collections have also been supplemented since 1933 by almost daily examination of living plankton catches over long periods.

These observations have now been made for 8 years, with the result that it is now possible to obtain a fair view of the medusa fauna in offshore waters off Plymouth and its changes from season to season and year to year.

The Plymouth Medusa Fauna

The "Plymouth Marine Fauna" (1931) records forty-one species of planktonic Hydromedusae, twenty-three Anthomedusae, fifteen Leptomedusae, two Trachymedusae and one Narcomedusa; four species of Siphonophora; and five species of planktonic Scyphomedusae. During the 8 years' observations since 1930 nine more species have been added to the fauna, viz.:

Anthomedusae: *Turritopsis nutricula* McCrady, *Pochella polynema* Hartlaub.

Leptomedusae: *Eucheilota clausa* (Hincks), *Helgicirrha schulzei* Hartlaub, *Aequorea vitrina* Gosse.

Trachymedusa: *Gossea corynetes* (Gosse).

Siphonophora: *Muggiaea kochi* (Will).

Scyphomedusae: *Pelagia noctiluca* Péron & Lesueur, *Discomedusa lobata* Claus.

Since 1930 I have myself taken all the species recorded at Plymouth except *Eucodonium brownei*, *Mitrocomella fulva*, *Solmaris corona*, and *Cyanea capillata*. (The specific names used in this report are those of the Plymouth Marine Fauna, except for *Zanclea* and *Eirene*.) The Siphonophora and Scyphomedusae are not referred to here except in the lists on pp. 416 and 417.

During the course of these 8 years' observations many data have accumulated on the occurrence of medusae in the different months of the year. By combining these results with the records given in the Plymouth Marine Fauna it has been possible to produce in Table I a reliable guide showing in which months of the year any species of medusa may be expected to occur and in which month any species has been recorded as being abundant. In this table the species have been arranged approximately in the order of their geographical distribution from north to south, and it can be seen at a glance that the more northerly species are usually present in the plankton earlier in the year than the more southerly. Table I thus gives a picture of the seasonal progression of the composition of the medusa fauna off Plymouth. The seasonal sequence according to geographical distribution is to be expected on account of the seasonal range of the temperature of the sea off Plymouth, and in this respect it is in agreement with the results already published for the young fish (Russell, 1930–7, Vol. xx, p. 147). But the information given in

Table I does not necessarily mean that all the species mentioned are certain to be found in any year. It must be supplemented by a close examination of the distribution of the species both geographically and with respect to the movements of the water masses in the English Channel. But as our knowledge of the plankton content of the different types of water grows we are becoming better able to say which are the species that are most likely to occur off Plymouth during any month in which specimens are required.

TABLE I. SEASONAL DISTRIBUTION OF PLYMOUTH MEDUSAE

× recorded as present; **×** months of greatest abundance; N.B., northern boreal; B., boreal; S.B., southern boreal; S., southerly; C., cosmopolitan.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
ANTHOMEDUSAE													
Rathkea octopunctata	×	×	×	**×**	**×**	..	..	..	..	..	×	..	N.B.
Hybocodon prolifer	..	×	×	×	**×**	×	..	..	..	..	..	..	N.B.
Euphysa aurata	..	..	×	×	×	×	..	..	×	..	..	..	N.B.
Steenstrupia nutans	..	..	..	×	**×**	**×**	×	×	×	..	..	..	N.B.
Podocoryne areolata	×	..	..	..	..	×	..	×	×	..	..	..	?N.B.
Podocoryne carnea	..	×	×	..	..	..	×	×	..	..	..	..	C.
Bougainvillia principis	..	..	..	×	×	..	..	..	..	..	..	..	N.B.
Sarsia tubulosa	..	..	×	×	×	×	×	..	×	×	×	..	N.B.
Sarsia eximia	..	..	..	×	×	×	×	..	×	..	..	..	?N.B.
Bougainvillia britannica	..	..	..	×	**×**	**×**	×	..	..	..	..	..	B.
Ectopleura dumortieri	..	..	..	×	×	..	..	..	×	×	×	..	?S.B.
Willia stellata	×	×*	×†	×	×	×	**×**	..	**×**	×	×	×	?S.B.
Lizzia blondina	..	..	×	**×**	**×**	**×**	**×**	×	**×**	..	×	..	S.B.
Leuckartiara octona	..	×	×	×	**×**	**×**	**×**	**×**	**×**	×	×	..	S.B.
Bougainvillia ramosa	..	..	..	×	×	..	..	×	×	×	×	..	S.B.
Purena gemmifera	..	..	..	..	×	**×**	**×**	..	×	..	×	..	S.B.
Amphinema rugosum	..	..	..	×	**×**	**×**	**×**	×	×	×	..	..	?S.B.
Zanclea costata	..	..	..	..	×	..	×	×	×	..	..	..	?S.B.
Sarsia prolifera‡	..	..	..	×	×	×	**×**	×	×	×	**×**	..	S.
Dipurena halterata	..	..	..	×	×	×	×	×	×	..	..	..	S.
Purena strangulata	..	..	..	..	..	×	×	..	..	..	..	..	S.
Amphinema dinema	×	..	..	..	..	..	×	..	**×**	**×**	..	..	S.
Turritopsis nutricula	×	..	..	..	..	..	..	×	×	**×**	×	×	S.
Eucodonium brownei	..	..	..	..	..	..	..	..	×	..	..	..	?
Pochella polynema	..	..	..	..	×	×	..	..	..	..	..	..	?
LEPTOMEDUSAE:													
Tiaropsis multicirrata	..	..	×	×	..	..	..	..	..	..	..	..	N.B.
Phialidium hemisphericum	×	×	**×**	**×**	**×**	**×**	**×**	**×**	**×**	**×**	..	..	B.
Obelia spp.	×	×	×	**×**	**×**	**×**	**×**	**×**	**×**	**×**	**×**	..	C.
Phialella cymbaloides	..	..	×	×	**×**	×	×	..	×	×	..	..	?B.
Cosmetira pilosella	..	..	×	**×**	**×**	**×**	**×**	**×**	×		..	..	S.B.
Mitrocomella brownei	..	..	..	×	×	..	..	×	..	..	..	..	?S.B.
Mitrocomella fulva	..	..	..	..	×	..	..	..	..	..	..	..	?
Saphenia gracilis	×	×	×	×	**×**	**×**	**×**	×	×	×	×	..	S.
Eutima insignis	..	..	..	..	..	×	..	×	×	×	..	..	S.
Aequorea forskalea	..	..	×	×	×	×	×	×	×	×	×	×	S.
Aequorea vitrina	..	..	..	..	..	×	..	..	..	..	..	..	S.
Laodicea undulata	..	×§	×	×	×	×	×	**×**	**×**	×	×	..	S.
Eucheilota clausa	×	..	..	×	..	×	×	..	×	**×**	×	×	?S.
Helgicirrha schulzei	..	..	..	..	..	×	×	×	×	×	..	..	S.
Eirene viridula	..	..	..	..	..	..	×	×	**×**	**×**	×	×	S.
Octorchis gegenbauri	×	..	..	..	..	..	×	**×**	×	×	..	..	S.
Agastra mira	..	..	..	..	..	..	×	×	..	..	×	..	?
TRACHYMEDUSAE:													
Aglantha rosea	×	×	×	×	×	**×**	**×**	**×**	**×**	×		×	S.B.
Liriope exigua	×	×	..	..	×	×	×	**×**	**×**	**×**	**×**	**×**	S.
Gossea corynetes	..	..	..	..	..	..	×	×	×	×	×	×	S.
NARCOMEDUSA:													
Solmaris corona	..	..	..	..	..	..	..	..	×	..	..	..	S.

* Hydroid with medusa ready for liberation. (E. T. Browne, MS. notes, February 22 1899.)
† Liberated from hydroid, March 30 1936.
‡ Plymouth Marine Fauna gives Jan.–Oct.; this is possibly a misprint for Jun.–Oct.
§ February 21 1938 one specimen.

The late Mr E. T. Browne laid a very sound foundation for a comparison of the different areas of distribution on the south and western shores of the British

Isles by his careful and prolonged studies, especially at Plymouth, Valencia, Port Erin and Millport. In a comparison of the faunas of Plymouth and Valencia, Browne (1900) gave the following species as occurring at Valencia but not at Plymouth: *Bougainvillia pyramidata*, *Dipleurosoma typicum**, *Melicertum octocostatum*, *Laodicea undulata*, ? *Aequorea forskalea*, *Aglantha rosea* and *Gossea corynetes*. Of these only *Bougainvillia pyramidata*, *Dipleurosoma typicum* and *Melicertum octocostatum* now remain not recorded from Plymouth, but to the list of those found only at Valencia must be added *Leuckartiara nobilis* and *L. breviconis* (see Hartlaub, 1911). The only species recorded from Plymouth and not from Valencia are *Turritopsis nutricula*, *Pochella polynema*, *Eucheilota clausa* and *Helgicirrha schulzei*; of these the last three have been described as new species since Browne's observations were made and *Eucheilota clausa* has now been found at Valencia (see p. 432). Browne's observations at Valencia were further supplemented by the Misses Delap (1905, 1906).

Browne (1906) also made a comparison between the medusae recorded from the English Channel and those taken in the Bay of Biscay on the cruise of H.M.S. *Research*. Of those species living within 100 fathoms of the surface in the Bay *Aglaura hemistoma* and *Rhopalonema coeruleum* had not been recorded in the Channel and they still remain unrecorded from Plymouth.

But such faunistic comparison is not sufficient in itself; to it must be added a knowledge of the comparative abundance of the species in the different localities. Unfortunately, I cannot give numerical data for many of the smaller species, but data for all those species occurring in the stramin ringtrawl catches will be found in Tables II and III. From the examination of townet catches and of the previously published records a good idea can, however, be obtained as to which species are common and which scarce. But while one species may be common in one year it may be very scarce the next. A comparison of the Plymouth medusa fauna with that of other regions, coupled with a knowledge of the occurrence of the hydroids of some species and a critical analysis of the data in Table III, enables us now to explain to some degree these changes in the composition of the fauna from year to year. There are some species which can undoubtedly be regarded as visitors to the area, but owing to Plymouth's geographical position it is difficult to decide for all species which are visitors and which may be called truly indigenous. This circumstance is brought about by the complicated hydrographic conditions existing in the Channel area, and in order to understand the composition of the medusa fauna off Plymouth we must have some idea of these conditions.

Through oceanic circulation and wind effects there is a resultant flow of water through the straits of Dover into the southern North Sea. The supply from which this water is ultimately drawn enters the western mouth of the

---

* This species was recorded off Brighton in 1879 by Haeckel in his *System der Medusen*, p. 636.

Channel either from the west or the south-west. It is generally conceded that more water enters the Channel than can pass through the Dover straits, and this surplus probably drifts north-west or north past the Scillies—Land's End region, though the actual state of affairs here is still not clear (Carruthers, 1934). To the west of the mouth of the Channel is an anticyclonic swirl lying over the shallow continental plateau south of Ireland. This swirl varies in its extent and position; at times it appears to block the mouth of the Channel and at others it apparently retreats farther north, thus laying the Channel mouth open to more oceanic water from the south and south-west. When there is a strong flow through the Dover straits, water may move up Channel past Plymouth either from the swirl or from the ocean according to the conditions existing off the Channel mouth. In the Channel itself there must be a body of water constantly being added to from the west and dissipated to the east, or hemmed into the coast to allow for passage of more oceanic water. The circulation of water in the Channel itself is clearly very variable from time to time.

It has been shown (Russell, 1936 *a*) that the various water types carry their own faunistic associations of plankton or indicators and, of these, three types have so far been elucidated:

(1) "Channel" water, characterized by *Sagitta setosa* and a poverty of plankton.

(2) "Elegans" (swirl) water, characterized by *S. elegans* and a number of associated species and a rich plankton.

(3) "Oceanic" water, characterized by salps and doliolids and their associated fauna.

There have also been during the past 3 years indications of the possible existence of a fourth type in which there are always large numbers of pilchard eggs and few *Sagitta* of either species; but its relationship in the general scheme is not yet clear.

These different types have also different species of medusae associated with them, and it is this fact that makes the true character of the Plymouth medusa fauna difficult to decide. The "*elegans*" water for instance contains in the summer great numbers of *Cosmetira* and *Laodicea*. In years in which this water is drifted past Plymouth it is natural to suppose that a stock of their hydroids should be produced on the sea bottom off Plymouth. Thus if a period of several years of absence of "*elegans*" water off Plymouth follows there is at first a good stock of hydroids to liberate medusae, but the numbers of adult medusae thereafter decrease. Presumably there is either an insufficient food supply or the type of water is for some reason harmful and not many medusae grow to maturity. The stock of hydroids will thus gradually diminish, but it is unlikely that for common species sufficient time ever elapses off Plymouth to allow the stock to die out before there is an importation of large numbers of fresh medusae from the west.

Similarly *Turritopsis* appears to be a species characteristic of "Channel" water, associated with *Sagitta setosa*. In periods when Channel water predominates off Plymouth it is thus possible that a local population of *Turritopsis* hydroids may arise. But *Turritopsis* is never very abundant, so that it is probable that its hydroid may die out at Plymouth after a prolonged continuation of "*elegans*" conditions.

This colonization of the grounds by hydroids from drifting medusae must be constantly borne in mind, and it can be understood that it is difficult to decide which species can be regarded as permanently indigenous to the waters off Plymouth. Even such medusae as *Phialidium* and *Obelia*, which are always present, become much more abundant during periods of predominance of "*elegans*" water presumably on account of the increased supply of food.

With these difficulties in mind I have attempted to draw up the following preliminary list of Plymouth medusae divided into indigenous and visiting species and indicating whether they are common or scarce. It is likely that in time, as our knowledge of their distribution increases, more of those species here listed as indigenous will be shown to be visitors.

Indigenous

Common

*Sarsia prolifera**
Purena gemmifera†
*Steenstrupia nutans**
Hybocodon prolifer
*Rathkea octopunctata**
Lizzia blondina†
*Bougainvillia britannica**
*Amphinema dinema**
*Leuckartiara octona**
Phialidium hemisphericum†
*Phialella cymbaloides**
Obelia spp.†
*Eucheilota clausa**
*Saphenia gracilis**
*Eirene viridula**
Aurelia aurita
Cyanea lamarcki
Chrysaora isosceles

Scarce

Sarsia tubulosa
Sarsia eximia
Zanclea costata
Ectopleura dumortieri
Bougainvillia ramosa
Podocoryne carnea
Willia stellata
Mitrocomella brownei
Octorchis gegenbauri
Helgicirrha schulzei
Gossea corynetes

Very rare (position uncertain)

Eucodonium brownei
Pochella polynema
Mitrocomella fulva
Agastra mira

* Abundant at times. † Very abundant at times.

Visitors

Abundant at times

Amphinema rugosum
Laodicea undulata
Cosmetira pilosella
Aglantha rosea
Liriope exigua
Muggiaea atlantica
Muggiaea kochi

Common at times

Turritopsis nutricula

Scarce

Dipurena halterata
Purena strangulata
Euphysa aurata
Bougainvillia principis
Podocoryne areolata
Tiaropsis multicirrata
Aequorea forskalea
Aequorea vitrina
Solmaris corona
Pelagia noctiluca
Discomedusa lobata

The above visitors can probably be divided among the three types of water as follows:

"Channel"	"*Elegans*"	"Oceanic"
Turritopsis nutricula	*Dipurena halterata*	*Aglantha rosea*
	Purena strangulata	*Liriope exigua*
	Euphysa aurata	*Solmaris corona*
	Bougainvillia principis	*Muggiaea atlantica*
	Podocoryne areolata	*Muggiaea kochi*
	Amphinema rugosum	*Pelagia noctiluca*
	Laodicea undulata	*Discomedusa lobata*
	Cosmetira pilosella	
	Tiaropsis multicirrata	
	Aequorea spp.	
	Aglantha rosea	

The above lists require one or two words of comment. The reservation must be made that at any time occasional specimens of visiting species may be found, but their presence in larger numbers is a sure indication of water movement.

As regards the indigenous medusae this list needs the qualification that in some years, owing to certain hydrographical conditions (see p. 419), all species may appear to be scarce. As regards the *relative* abundance of the different species it should however still hold good.

The scarcity of *Sarsia tubulosa* and *S. eximia* in offshore waters is probably due to the very littoral or estuarine distribution of their hydroids. These are quite common inshore. It is also rather remarkable that while the hydroids of *Zanclea costata*, *Bougainvillia ramosa*, and *Podocoryne carnea* are common off Plymouth the medusae themselves seem to be rather scarce. It may possibly be accounted for by the fact that the medusae, especially those of *P. carnea*, may often mature at a very undeveloped stage, thus only being present in the plankton for a very short time.

It is also to be noted that in the above list *Aglantha rosea* has been included as an indicator both of "*elegans*" and of "oceanic" waters. *Aglantha* is essentially an oceanic medusa, nevertheless a large stock appears to flourish in the water south of Ireland. It may thus possibly be drawn from two sources, though results seem to show that it is more usually associated with "*elegans*" conditions.

Euphysa aurata and *Bougainvillia principis* have never been recorded commonly off Plymouth, yet they are common south of Ireland. The reason for their continuous scarcity at Plymouth is not clear.

The occurrence of the oceanic indicators is not yet fully elucidated. For instance, *Liriope* has so far only appeared abundantly off Plymouth during periods of essential "*elegans*" predominance (see p. 423).

Before passing on to the details of the ringtrawl catches mention should be made of an interesting feature of the Plymouth medusa fauna as a whole. This is that of the northern species by far the majority are Anthomedusae. This fact led me to make a casual survey of the medusae of cold waters (see e.g. Thiel, 1932; Browne, 1902, 1910). It is evident that of the medusae liberated from hydroids the majority in cold waters are Anthomedusae or so-called "primitive" Leptomedusae such as laodiceids and mitrocomids. This difference between the medusa faunas of cold and warm waters seems worthy of a closer investigation. In this respect it is interesting to note that all the laodiceids and mitrocomids whose hydroids are so far known have "*Cuspidella*" hydroids. It may well be that this is the primitive type from which many of the campanulate hydroids have evolved and that the evolution of the Leptomedusae has taken place mainly in warm waters. Being of more recent evolution than the Anthomedusae they have not yet given rise to many cold-water species.

The Ringtrawl Catches, 1930–7

The average catches for each month in the years 1930–7 are given in Table III, p. 436. These are based on half-hour oblique hauls taken usually each week at a position 2 miles east of the Eddystone (for the actual dates of hauls see Russell, 1930–8). The sums of the average monthly catches of each year are given in Table II.

Before discussing the results of these collections a few remarks must be made on the identification of species. As already mentioned, owing to the size of the mesh employed only the larger species are represented in these catches. Such species as *Purena gemmifera*, *Rathkea octopunctata* and *Lizzia blondina*, the majority of which are not retained by the net, have not been counted, although when they are very abundant in the plankton a few may be found in the catches. Owing at times to the large masses of other plankton animals in the catches the medusae are often in a very bad state of preservation, and when numerous themselves could not be subjected to so close a critical examination as is to be desired. Long experience of dealing with such catches in bulk has, however, enabled me to be fairly certain that the identifications are correct, and the re-examination at a later date of previously sorted material, and frequent observations of living samples taken at the same times as the catches which were preserved, have convinced me that a reliable picture has been produced of the medusa fauna taken by the ringtrawl. There are, however, one or two species that can only be separated for certain by a critical examination under the microscope. These are *Mitrocomella brownei*, *Eucheilota clausa* and *Phialella cymbaloides*, which in bulk catches sorted with the naked eye may easily be mistaken for *Phialidium hemisphericum*. No regular attempt was made to discriminate between these species and all have been counted under *Phialidium*. As *Phialidium* is by far the most abundant the inclusion of the other species has probably not produced a very false impression. Of the other species *Phialella cymbaloides* and *Eucheilota clausa* are quite common at times, but *Mitrocomella brownei* is scarce. *Saphenia gracilis* and *Eutima insignis* have also been counted together as *Saphenia*. They are often in too bad a state to be sure of the number of tentacles as the manubria become twisted together, and it is indeed uncertain whether they are distinct species.

When we examine the results as a whole (see Table II) the most striking feature is the great decrease in the numbers of total medusae in the years 1935, 1936 and 1937 as compared with the previous years. The high numbers in the years 1930, 1931 and 1932 are in part made up by the abundance of *Laodicea*, *Cosmetira*, *Aglantha* and *Liriope*, which were visitors to the area associated with the predominance of "*elegans*" and "oceanic" water. But when we regard the commonest truly indigenous species, such as *Leuckartiara*, *Phialidium* and *Obelia*, we notice that in the later years there has on the whole been a great decrease in numbers. The decrease in the numbers of young fish in the plankton during this period has already been noted (Russell, 1936 *a*), and there can be little doubt that the decrease in numbers of medusae is an associated phenomenon. At the foot of Table II are included the corresponding numbers for all young fish (less clupeids) taken in the same series of collections. The low numbers of young fish in the years 1935, 1936 and 1937 closely parallel those for the medusae. The abundance of young fish has been shown to follow closely the winter maximum of phosphorus content of the water (Russell, 1936 *a*), and it seems quite evident that this lack of nutrient matter has resulted in a decreased supply of planktonic food for such predatory organisms as fish and medusae and affected their survival rate.

TABLE II. SUMS OF AVERAGE MONTHLY CATCHES OF MEDUSAE IN THE RINGTRAWL FOR EACH YEAR AT PLYMOUTH

	1930	1931	1932	1933	1934	1935	1936	1937
Steenstrupia nutans	46	123	64	18	1,232	6	15	59
Bougainvillia britannica	296	112	402	4	1,285	33	2	2
Turritopsis nutricula	..	..	..	17	1	3	25	34
Amphinema dinema	..	..	6	8	7	107	55	70
Amphinema rugosum	473	1	21	13	2	..	7	2
Leuckartiara octona	658	513	403	218	108	102	68	16
Laodicea undulata	5,141	2,527	22	70	282	208	4	18
Cosmetira pilosella	891	2,111	2,599	326	342	41	6	7
Obelia spp.	15,418	1,311	18,656	2,730	13,649	1,935	797	2,151
Phialidium hemisphericum	8,950	12,554	5,862	9,512	5,179	600	948	2,605
Saphenia gracilis	157	22	28	67	34	39	136	108
Octorchis gegenbauri	..	28	+	8	10	36	14	25
Eirene viridula	..	1,314	83	56	1	7	2	39
Helgicirrha schulzei						3	2	1
Aequorea forskalea	+	13	4	..	+	1	2	+
Gossea corynetes	..	12	1	4	11	6	1	13
Aglantha rosea	38,439	143	..	1	32	22	425	60
Liriope exigua	15,522	327	..	3	+	+	..	..
Total medusae	85,991	21,111	28,151	13,055	22,175	3,149	2,509	5,210
Total young fish (less clupeids)	1,517	1,625	1,556	1,337	1,144	430	487	557

If we examine the list in Table II in greater detail other points of interest are to be found. In the year 1934 *Steenstrupia nutans* and *Bougainvillia britannica* were both unusually abundant; in that year there were more *Sagitta elegans* present in May than in recent years. The sudden appearance of *Turritopsis* in 1933 and its persistence thereafter is to be associated with the prevalence of Channel water. There has been a sudden increase in abundance of *Amphinema dinema* in 1935, 1936 and 1937, while *A. rugosum* was very abundant in 1930 during the year of greatest "*elegans*" predominance. The year 1931 was outstanding for the numbers of *Eirene viridula*; it is to be noted that this abundance coincided with the presence of *Salpa mucronata* and *Doliolum gegenbauri* which occurred only in that year. No attempt can be made to explain all these differences from year to year, but they are here noted for comparison with future years.

Observations on Certain Medusae

In the following pages are given further details on the biology of some of the Plymouth medusae together with a few observations of note on structural details.

Purena gemmifera (Forbes).

I have noticed that the tentacles of living medusae of *Purena gemmifera* show a characteristic vibrational movement. This movement is produced by cilia on the tentacles. These cilia which appear to be confined to the nematocysts clusters and terminal knob can already be seen on the tentacles while the young medusae are still attached to the stomach of the parent. A careful examination of living specimens of other medusae has so far shown no similar ciliation in other Sarsiid species.

Zanclea costata Gegenbaur.

In a previous publication (Russell & Rees, 1936) *Zanclea gemmosa* McCrady with two tentacles was provisionally kept distinct from *Zanclea costata* Gegenbaur until it could be shown either that the latter was liberated from the hydroid with four tentacles, or that a medusa with four tentacles could develop from one with two. In 1937 I obtained a complete series of *Zanclea* medusae from the plankton showing the development of a two-tentacled medusa into one with four tentacles. Among these specimens a medusa 1·5 mm. in height had two opposite perradial tentacles, another 2 mm. in height had two fully grown opposite perradial tentacles, and on the other two perradial bulbs there were very short tentacles just developing. Another 3·1 mm. in height had four tentacles of nearly equal size. There seems therefore to be little doubt that the medusae with two and those with four tentacles are the same species and referable to *Zanclea costata* Gegenbaur.

It is hoped to deal with the questions raised by Weill (1936) and Ranson (1937) about the nematocyst armature on the umbrella in a future publication.

Bougainvillia britannica Forbes.

The year 1934 was outstanding for the abundance of this species and the presence of such large numbers furnished an opportunity to study the growth and development of the medusa in the plankton. Measurements of height and width were made on a large number of preserved specimens from the plankton on April 20 and May 3, 16 and 24. The actual period when the medusae were present in the plankton and their numbers in the weekly catches were as follows:

April 6	10	May 2	1567
„ 12	4	„ 9	41
„ 16	4	„ 16	2731
„ 26	233	„ 24	1528
		„ 29	244

When alive the medusa is usually somewhat higher than it is wide; when preserved, however, contraction causes them often to be as wide as they are high. In order to range the medusae after measurement the height of each specimen was multiplied by its width and the square root of the product taken. Thus the measurements of the medusa diameter given in the table on p. 422 and Fig. 1 are for spherical medusae and would probably have been very slightly greater if the measurements of height had been made on living material. The data have been supplemented by some material collected on April 20 when the ringtrawl was not used.

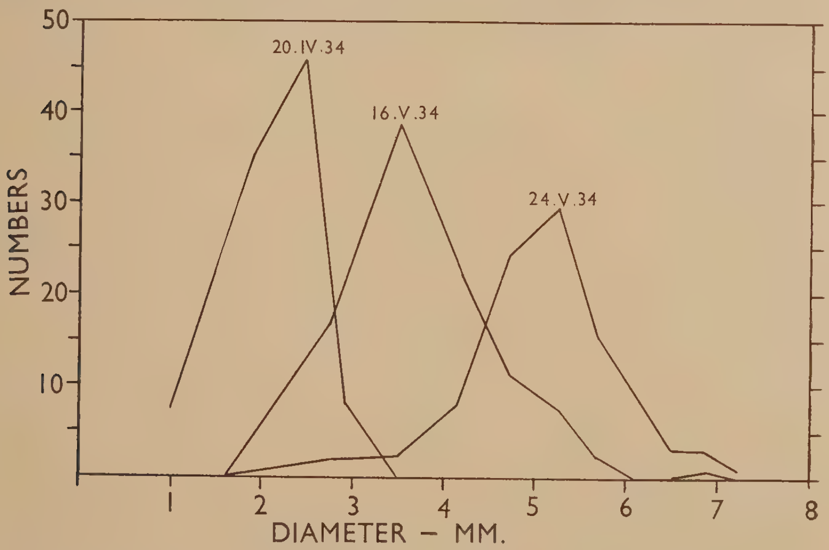


Fig. 1. Growth of *Bougainvillia britannica* from samples collected in the plankton off Plymouth, 1934. The curves show the numbers of specimens of different diameters on April 20, May 16 and 24.

Growth. The results of measurements made on April 20, May 16 and 24 are shown in Fig. 1. The growth of the medusae is well illustrated, the mode increasing successively from 2·5 to 3·5 and 5·25 mm. on each successive date. The maximum size attained is about 7 mm. The medusa had disappeared from the plankton completely by June 6. Thus the period from the date of first appearance (April 6) was 2 months. By May 16 some of the gonads were mature and planulae were reared. The dates of appearance of the medusa in the plankton coupled with the gradual increase in size shown in Fig. 1 afford fair evidence that the length of life of the medusa *Bougainvillia britannica* in Plymouth waters is not more than 2 months. Kramp (1927) has said that in Danish waters "it lives presumably for about 2 months, but we know nothing certain as to this".

Development. The medusa when first liberated from its hydroid has four single marginal tentacles and four unbranched oral tentacles. As growth proceeds the number of marginal tentacles increases on each of the four tentacular bulbs and the oral tentacles branch dichotomously. Observations were made on a large number (140) of medusae of different sizes and the sequence of their development found. The examination gave the following results:

Diameter (mm.)	Number of tentacles on each marginal bulb	Number of times oral tentacles are branched
1·5	3	1–1(+)
1·75	3– 4	1–2
2·0	4– 5	1–2(+)
2·25	4– 5	(1)–2
2·5	4– 6	(1)–2–2(+)
2·75	5– 6	2
3·0	5– 7	2
3·25	5	2
3·5	8– 9	3
4·0	9–11	3–3(+)
4·5	10–11	3(+)–4
5·0	10–12	3(+)–4
6·0	11–13	4–4(+)
7·0	14–15	4
7·5	16–17	5(+)

Note. (+) implies that some of the branches are just starting to subdivide. Numbers in brackets are exceptional occurrences.

It is evident from this table that full-grown medusae will have about eleven to seventeen tentacles on each marginal bulb, and the oral tentacles will be dichotomously branched four or five times. This agrees with observations by Hartlaub (1911) on a swarm in the North Sea. His specimens had well-developed gonads and averaged 5–7 mm. in height, and the number of tentacles on each marginal bulb averaged twelve to sixteen. Hartlaub gives 12 mm. in height as the largest size, the tentacles on each marginal bulb up to 30 in number, and oral tentacles branching at most seven times. Such individuals must be exceptional.

Bougainvillia principis (Steenstrup).

This species appears to be very rare at Plymouth. One specimen was taken in May 1935, one* in May 1936 and one in April 1937. The only previous record is the end of April 1893 (Garstang, 1894). In its distribution it is much more northerly than *B. britannica*, although it occurs more commonly at Valencia than at Plymouth.

Turritopsis nutricula McCrady.

This species has not been recorded in the Plymouth fauna prior to this series of observations. It was first seen in 1933, and has occurred each year since. The species is indigenous in the southern North Sea and eastern end of the English Channel, where it has been used by Kramp (1930), Wulff, Bückmann, and Künne (1934) and Künne (1937) as an indicator of water movements. Its first appearance here and its continuation is coincident with the decrease in "*elegans*" water which has been so noticeable after the year 1932. Browne (1898) did not find the species at Plymouth in the years 1893, 1895 and 1897 although working in September, a month in which *Turritopsis* occurs in the plankton. Browne's records show that those years were characterized by the presence of *Liriope*; this would explain the absence of *Turritopsis* at that time, since *Liriope* has only appeared in numbers during the last eight years in 1930–1 when "*elegans*" conditions were most predominant. Künne (1934) states that *Turritopsis* penetrated farther into the southern North Sea in 1932 than in 1933, in which year it appeared off Plymouth.

There has in the past been some discussion as to the identity of the European species of *Turritopsis*, which was described under the specific name *polycirrha*. Although Mayer (1910) could detect no specific differences between *polycirrha* and the American *nutricula*, Hartlaub (1911) kept them distinct. He maintained that in *polycirrha* the endodermal mass was not in four sections, and that the radial canals did not penetrate the endodermal mass or widen into chambers as figured by Brooks. Later (1917) he recorded a specimen from Heligoland that agreed with Brooks' figure as regards the widening of the radial canal, though he maintained that the identity of the two species still remained unproved. Their identity has, however, been accepted by Mayer (1910), Bigelow (1913) and Kramp (1930); it is accepted here on the grounds that all specimens seen at Plymouth showed the endodermal mass divided into four sections which were traversed by the radial canals. Cavities were also frequently seen in the endodermal mass, which when radially disposed could give rise to the appearance figured by Brooks.

Amphinema rugosum Mayer.

In earlier literature there has been considerable confusion between this species and *A. dinema* (see Rees and Russell, 1937). Since I was myself at first confused by Hartlaub's (1911) description of one species under the name of the other I have found it necessary to re-examine all the previous samples on which any data have been published; as I expected to find, all species under the specific name *dinema* should have been *rugosum* (a revision of my data will be found in the footnote*).

---

* I am indebted to Dr P. L. Kramp for confirmation of the identification of this specimen.

From the occurrence of *A. rugosum* in such numbers in 1930 it appears probable that the species is associated with "*elegans*" conditions. The true distribution of the species is not yet known, but in 1933 while cruising in Col. E. T. Peel's yacht *St George* I took a plankton sample on July 9 at a position north of the Fair Isle Channel (59° 42′ N.; 2° 10′ W.). This was a typical *elegans* association and there were a number of *A. rugosum* present. The species is therefore not likely to be normally indigenous to Plymouth, and it is perhaps significant in this respect that the only two records of its hydroid off Plymouth are on floating objects that may have drifted into the area (see Rees and Russell, 1937).

A detailed examination was made of a number of specimens taken off Plymouth in June and July 1930. The numbers of marginal tentaculae were counted on sixty-three specimens with the following results:

Total number of marginal tentaculae	Number of individuals	Distribution of tentaculae on either side of large tentacles	Number of individuals
11	1	5+6	1
12	2	5+7	1
13	6	5+8	1
14	14	6+6	1
15	10	6+7	5†
16	7	6+8	1
17	8	7+7	13
18	4	7+8	10
19	4	7+9	2†
20	1	8+8	5
21	3	8+9	8
22	3	8+11	1
		9+9	4
		9+10	3
		9+12	1
		10+10	1
		10+11	2
		11+11	3

† One abnormal.

From these figures it is evident that there is considerable variation in the number of tentaculae, which have been recorded up to twenty-four in number, the most frequent numbers here being fourteen to seventeen. The number must naturally vary with the age and size of the medusa, but the preserved specimens were too contracted to measure.

---

* I have examined the medusae in my collections and find that in all my previously published papers the medusae recorded under the names *Stomotoca dinema* or *Amphinema dinema* were in fact *A. rugosum*. These records are in this *Journal*, Vol. XIII, p. 781, July 15–16 1924; Vol. XIV, p. 569, June 17, 19; July 1, 16, 29 1925; Vol. XV, Table I, June 17, 18, 19 1925; Vol. XIX, Table I, June 10, 19, July 14, 23, 29, August 14 1930.

An analysis of the distribution of the marginal tentaculae gives the following results:

Equal numbers on either side of two main tentacles	27
A difference of one on either side of two main tentacles ...	28
A difference of two on either side of two main tentacles ...	3
A difference of three on either side of two main tentacles ...	3

Thus it appears that the normal increase of the number of tentaculae is by the addition of one tentacula at a time on either side of the medusa.

A. rugosum appears to be rather prone to abnormality. Of the two abnormal specimens mentioned in the above table, one had the following arrangement: one large tentacle with single radial canal, eight marginal tentaculae with no radial canal, one large tentacle with radial canal which bifurcated near its origin from the stomach with the two branches rejoining at the tentacle bulb, one marginal tentacula, one half-size large tentacle with a radial canal, eight tentaculae with the normal radial canal among them. In the other, one of the tentacular radial canals had bifurcated giving rise to a fully developed large tentacle at the end of each branch; its arrangement was one large tentacle, two tentaculae, one large tentacle, five tentaculae, one large tentacle, seven tentaculae. Other abnormal specimens were seen, one in which there was only one large tentacle, the place of the missing tentacle being taken by a tentacula; and two in which there were three large tentacles, in one of which the additional large tentacle was adradially situated and not opposite a radial canal.

Pochella polynema Hartlaub.

In May 1934 a specimen of *P. polynema** was taken off Plymouth. The medusa (Fig. 2*a*) was 2·7 mm. in diameter; it had thirty tentacles, fifteen large and fifteen small, each springing from a brown marginal bulb. The four radial canals were not observed to be branched, and the preserved specimen is too contracted to show branches if they were present.

This species was described by Hartlaub (1917) from seventeen specimens collected from the northern North Sea in June 1905. It has never been recorded since from European waters.

In 1936 while I was in Edinburgh Mr P. Gray showed me a number of slides of medusae that he had collected from the Firth of Clyde. Among these were two labelled *Pochella? polynema*. Mr Gray very kindly gave me one of these slides, a drawing of which is reproduced in Fig. 2*b*. This specimen, a female collected in Loch Fyne in April 1934, has twenty-seven tentacles, sixteen of which are large and eleven smaller. It is 2·4 mm. in height (mounted on slide). The ovaries are interadially situated on the stomach. The solid core of endoderm cells in the tentacles is to be clearly seen.

* Is this *Oceania pusilla* of Gosse, "Devonshire Coast", 1853, p. 384, Pl. 13, figs. 11–14?

There can be little doubt that these specimens are the same species as Hartlaub's medusae.

Hartlaub states that occasionally the radial canals were branched, the branches starting about at the middle of the canal and running outwards towards the umbrella edge; some were short and blind, and some longer. In the mounted specimen that I have there is definitely no branching of the radial canals. When, however, I showed these medusae to Mr E. T. Browne he turned up from his collection two specimens taken 40 years ago at Plymouth and labelled by him as a new species of *Proboscidactyla*. These specimens differ in no respect from mine except that very delicate branches can be seen on some of the radial canals, much as described by Hartlaub. The specimens are too contracted to allow detailed observation of the branching system.

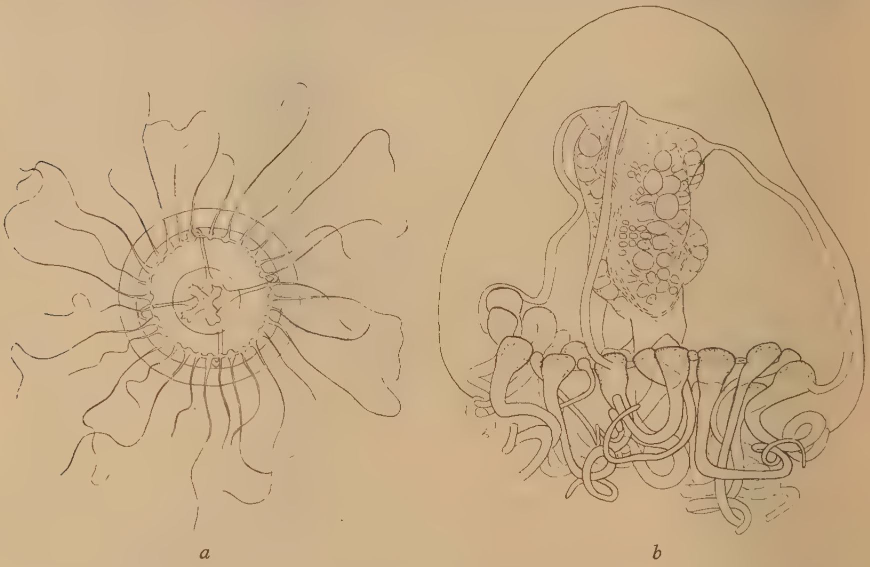


Fig. 2. *Pochella polynema*. *a*, living medusa 2·7 mm. in diameter caught off Plymouth May 25 1934. *b*, mounted specimen collected by Mr P. Gray from Loch Fyne, April 1934.

One of the specimens, taken by Mr Browne on June 30 1898, is 2·0 mm. in height (preserved in formalin) and has thirty-two tentacles, larger and smaller ones approximately alternating. It is a mature male. The four gonads are situated on the interradii of the stomach (Fig. 3*a*). Two opposite gonads have the form of large cushions with their thickest parts at the upper ends. The other two gonads are thickest at their lower ends so that when viewed laterally they may be seen projecting as lobes on either side of the lower halves of the other two gonads (Fig. 3*b*). The other specimen, taken on May 26 1898, is 1·4 mm. in height (preserved in alcohol) and has thirty-three tentacles.

In none of the above specimens was there any indication of exumbrella nematocyst canals, neither did Hartlaub find any. Until more specimens are obtained we cannot state whether the ring canals are solid. The systematic position of this species still remains problematical until more of its life history is known. There is, of course, the possibility that the medusae with unbranched radial canals may be different species from those in which the radial canals are branched. The fact that Hartlaub caught his seventeen specimens all together, some of which were with branched canals and others without, rather suggests, however, that they were all one species.

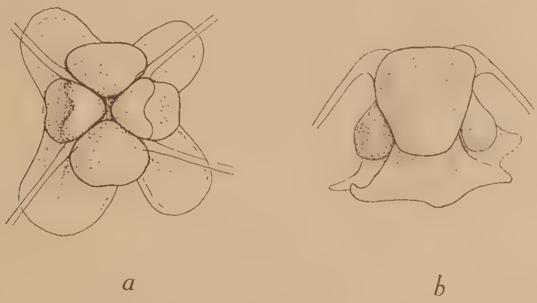


Fig. 3. *Pochella polynema*, Plymouth, June 30 1898 (E. T. Browne's collection). *a*, aboral view of gonads; *b*, lateral view.

The species has been recorded from Departure Bay, on the Pacific coast of North America, by Foerster (1923, p. 30), who called it *Proboscidactyla polynema*. In his specimens there were fine thread-like branches from the radial canal "invisible except under the high power of the microscope". The medusae were 2–4 mm. in diameter and there were 12 tentacles in each quadrant.

Foerster placed the species in the genus *Proboscidactyla*, but the gonads are not radial outgrowths from the stomach, neither are there exumbrella nemetocyst channels. On account of these differences it seems better to keep the genus *Pochella* distinct. In its affinities it is perhaps nearest to the Williidae, and if future research should show that it belongs to that family the characters of the family will have to be emended to take it.

Laodicea undulata (Forbes & Goodsir).

The probability that *L. undulata* cannot be regarded as a truly indigenous species off Plymouth has already been mentioned (p. 415). Kramp (1930) concluded that the species was indigenous in the southern North Sea because it was abundant in 1906, a year in which the influx of water from the Channel into the North Sea was only slight. It is, however, noteworthy that 1906 was the year following two successive years, 1904 and 1905, in which the influx was above the normal. It is thus possible that this may have been an instance of hydroids having developed on the sea bottom from mature medusae carried into the area in previous years. Kramp states that the medusae produced in the southern North Sea were considerably dwarfed, the majority being less than 8 mm. in diameter. In 1937 none of the *Laodicea* seen off Plymouth exceeded 7 mm. in diameter, and it appears that this is a parallel phenomenon with that observed by Kramp. It is probably an indication that the conditions of Channel water are not suitable for the successful growth of the medusa. In years when *Laodicea* occurs off Plymouth in large numbers the medusae are up to 15–20 mm. in diameter.

Cosmetira pilosella Forbes.

Two species of *Cosmetira* are recorded from the north Atlantic, *C. pilosella* Forbes and *C. megalotis* (Maas). The usual distinctions given between these two species in recent literature are (see e.g. Hartlaub, 1909, and Kramp, 1933):

	C. pilosella	*C. megalotis*
Umbrella diameter	*ca.* 20 mm.	30–40 mm.
Number of tentacles	*ca.* 64	*ca.* 100
Gonads/radial canal	$\frac{3}{4}$	$\frac{1}{3}-\frac{1}{2}$

This appears to overlook Forbes' (1848) original description of *C. pilosella* in which he gives the number of tentacles as (24 × 4 + 4), i.e. 100, and whose figure of the medusa shows at least eighty-two tentacles.

Diameter mm.	Tentacles and Developing Bulbs									Length of gonad mm.	Sex
	Numbers between every two marginal vesicles								Total		
15	8	8	9	7	8	8	12	8	68	6	♀
15	11	7	9	6	11	6	11	6	67	4	♀
16	11	6	10	6	10	9	11	8	71	4	♂
16	13	10	12	11	11	9	12	10	88	6·5	♂
16	13	11	12	9	13	9	11	11	89	. .	. .
17	12	9	13	11	25*	20*			90	5	
17	10	11	7	11 : 2† :7		11	8	8 : 1†	76	5	♂
17	10	9	12	9	11	15*	8		74	5	♂
18	12	13	10	12	10	11	11	13	92	7	♂
18	11	12	13	14	8	15	7	12	92	7	♂
18	10	8	12	9	9	8	11	9	76	5·5	♂
18	10	8	9	7	13	11	11	8	77	6	♂
18	11	8	12	8	13	9	12	8	81	5·5	♂
18	11	11	12	21*	10	11	8			6·5	♀
19	10	10	12	11	16	10	14	10	93	Short	♂
19	11	7	7	9	12	8	11	7	72	5	♂
19	13	12	12	11	13	11	16	11	99	7	♂
19	13	9	10	9	10	9	12	9	81	6·5	♀
20	11	9	11	11	11	8	10	9	80	5·5	. .
20	12	7	12	7	13	8	9		68	5·5	♂
21	12	9	13	9	12	8	11	8	82	6·5	♂
21	15	3	15	11	11	9	11	10	85	8·5	♀
22	13	7	10	4	10	8	10	6	68	4·5	
22	11	11	11	10	9	8	8	9	77	7	♂
22	13	11	12	9	12	8	12	8	85	6	♂
23	11	10	8	12	11	9	11	9	81	. .	. .
23	11	9	11	10	12	9	11	9	82	7	. .
24	10	8	12	8	14	9	19*		80	7	♀
24	11	9	13	9	12	10	11	12	87	8	♂
26	10	9	14	9	20*	10	7		79	8	♂

* Marginal vesicle missing. † Extra marginal vesicle.

On August 17 1932 a number of *C. pilosella* caught off Plymouth were preserved for careful examination. The results are shown in the above table, in which are given the diameter of the medusa, the numbers of tentacles and developing bulbs between every two marginal vesicles beginning with a radial canal octant, the total number of tentacles and bulbs, and the lengths of the gonads.

This table shows that the diameters of the medusae varied between 15 and 26 mm., and that the numbers of tentacles and bulbs ranged from sixty-seven to ninety-nine. The length of the gonads varied from 0·2 to 0·4 of the diameter of the umbrella, or taking the radial canal length as approximately half that of the umbrella *ca.* 0·4–0·8 of the radial canal, or slightly less allowing for the width of the stomach. It is probable that in the preservation some medusae have contracted more than others.

Thus the number of tentacles and size of the gonads of *C. pilosella* at Plymouth overlap those given for *C. megalotis*, and the only remaining difference between the two species is in the size of the umbrella. Incidentally in this respect the Misses Delap (1905) record specimens from Valencia up to 48 mm. in diameter which were fully mature.

Künne (1937), using *Cosmetira* as an indicator of northern water in the southern North Sea, decided that his specimens were *C. megalotis*. While cruising in Col. Peel's yacht *St George* in 1933 I obtained some specimens of *Cosmetira* from north of the Fair Isle Channel (July 9 1933; 59° 42′ N., 2° 10′ W.). The diameters, numbers of tentacles and bulbs, and length of gonads (when not lost) were as follows:

mm.		mm.
15	63	..
15	68	..
15	71	4·5
17	80	5·5
18	81	..
19	84	7·5

These figures agree closely with those for the Plymouth medusae, and there can be no doubt that they were *C. pilosella*.

Tiaropsis multicirrata (M. Sars).

This species has only once been recorded at Plymouth: by Dr E. J. Allen in April 1895. On April 21 1934 a very small specimen was taken in the Sound. This was 1·39 mm. high and 1·25 mm. wide and had about twenty-four tentacles. The presence of so small a specimen must have been an indication that the hydroid was living in the locality. Its hydroid is unknown, but the extreme rarity of the medusa shows that it cannot normally be indigenous off Plymouth.

Phialidium hemisphericum (L.).

Phialidium is, with *Obelia* spp., by far the commonest species of medusa off Plymouth, and it may be taken in any month of the year. There is, however, a great decrease in numbers in the winter months, and it may sometimes be entirely absent in January and February. Observations by Orton (1920) showed that its hydroid, *Clytia johnstoni*, liberates medusae from March to October, and I have seen them liberated in November.

Two rather different forms are found in the plankton: a large form with elongated gonads, especially in the spring and early summer, and a small form with short oval gonads in the autumn. This has in the past given rise to the idea that there may be two species (see Browne, 1896, p. 489), but it is now generally agreed that there is only one. The difference is due to seasonal variation in size and the following observations confirm this.

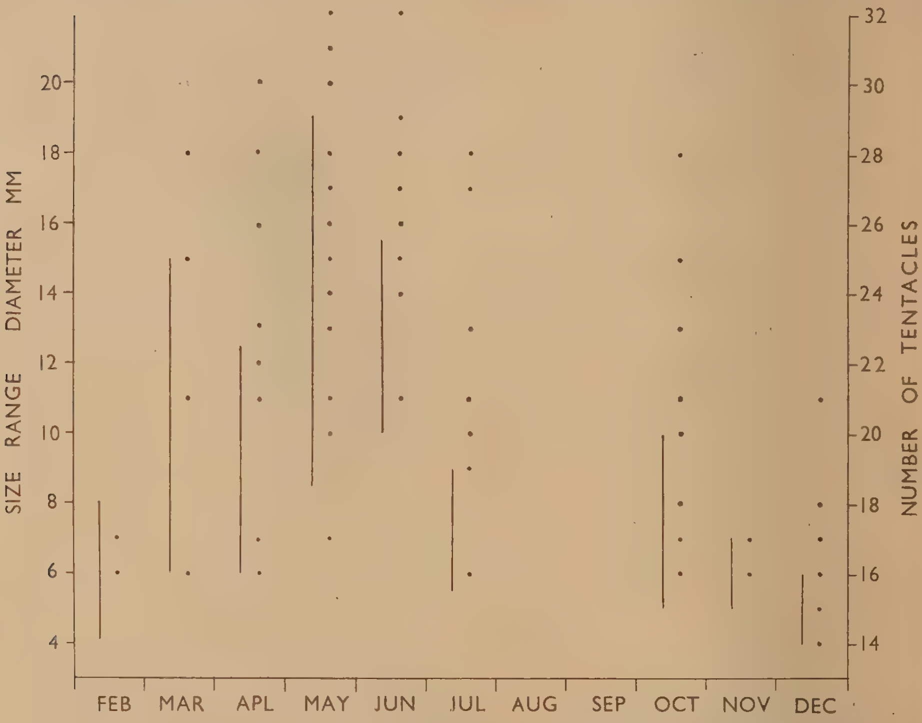


Fig. 4. Seasonal variation in diameter and number of tentacles of *Phialidium hemisphericum* in the plankton off Plymouth 1933 and 1934. The continuous lines show the size range and the dots the range of tentacle numbers.

During 1933 and 1934 a large number of living *Phialidium* were measured and their tentacles counted. The results are given in Fig. 4, which shows the size range for mature medusae in each month of the year (except August and September) and the numbers of tentacles (including developing bulbs) that they had. It shows clearly that in the spring and early summer the medusae grow to a larger size than at other times of the year. The maximum size reached was 19 mm. diameter in May. Also, as might be expected, the largest medusae have the greatest number of tentacles. These reached a maximum of thirty-two in May and June, while by October they were usually sixteen to eighteen fully formed tentacles, any larger numbers being made up with developing bulbs.

Browne (1900) found that at Valencia the largest specimen taken, in May, was 20 mm. in width and had thirty-eight tentacles, the average size of the adult being 10–15 mm. with about thirty-two tentacles. Similarly at Port Erin (1896, p. 490) he found the largest specimen to be 21 mm. and to have thirty-eight tentacles.

As observed by Browne I have occasionally seen specimens at Plymouth having one or two marginal vesicles containing two concretions. The largest number of marginal vesicles seen in any one specimen at Plymouth was eighty-nine (two of which each had two concretions); this was in a specimen 19 mm. in diameter taken on May 15 1934, which had thirty-two tentacles.

Measurements made on the gonads of medusae of different sizes gave the following results:

Umbrella diameter mm.	Gonad length (mm.)			Ratio diameter*: av. gonad length
	Average	Range	Observations	
4·1–5	0·30	0·21–0·76	11	15·0
5·1–6	0·59	0·4–0·75	15	9·3
6·1–7	0·67	0·3–1·1	17	9·9
7·1–8	0·98	0·75–1·5	6	7·7
8·1–9	0·94	0·5–1·5	8	9·0
9·1–10	1·26	0·5–3·0	13	7·5
10·1–11	1·25	0·75–2·0	8	8·4
11·1–12	1·43	1·0–2·0	14	8·0
12·1–13	1·64	1·0–3·0	13	7·6
14·1–15	1·75	1·5–2·0	2	8·3
15·1–16	2·1	1·5–3·0	7	7·4
16·1–17	2·25	2·0–2·5	2	7·3
18	3·0		1	5·8
19	3·5		1	5·4

* Diameters taken as 4·5, 5·5, 6·5, 7·5 mm., etc.

Except for the smallest and the largest individuals the ratio of the average gonad length to the umbrella diameter thus appears to be fairly constant with a slight tendency to decrease with size. The figures for the smallest specimens are probably vitiated by the inclusion of immature specimens, while those for the two largest sizes are each based on a single observation.

The above observations on size of medusa, number of tentacles and gonad length, are somewhat different from those given by Kramp (1927) for Danish waters. There, while the smaller specimens (6–7 mm. diameter) occurred in summer, the larger specimens (11–12 mm. diameter) were found in winter, though they reached 16 mm. in spring. While in July the number of tentacles rarely exceeded sixteen, in November they were as a rule twenty-four to twenty-eight. Kramp also says that the gonads are about one-quarter the length of the radial canals. This agrees approximately with the results for Plymouth, where the gonad length averages about one-eighth of the diameter of the umbrella of which a radial canal occupies approximately one half.

Kramp (1927) pointed out that the ratio of the width to the length of the gonads varied at different times of the year. Assuming that there is no very great difference in the size of the eggs at different times of the year it seems natural to expect the smaller gonads to be wider in relation to their length than the longer gonads.

The trend of the seasonal change in size at Plymouth is quite what is to be expected from observations on other plankton animals such as *Calanus*, *Sagitta* and *Aglantha*. It is shown by *Phialidium*, since this is one of the few medusae apart from *Obelia* which is consistently liberated from its hydroid into the plankton almost all the year through. It seems probable that *Obelia* should also show similar seasonal variation but this cannot be proved owing to the difficulty of identifying the species.

Eucheilota clausa (Hincks).

The existence of this species at Plymouth has only recently been brought to notice (Russell, 1936 *b*, *c*). Other records of its seasonal occurrence have since been obtained and these have been incorporated in Table I. As the distribution of the species is not known the following information is worthy of note. In September 1936 I received a letter from Mr J. S. Barlee saying that he had caught a specimen 1 mm. in diameter at Valencia. On September 10 he obtained two specimens, 1 and 4 mm. in diameter respectively, in Dalkey Sound, Co. Dublin, and on September 15 a dozen larger specimens off Sandycove, near Kingstown, Co. Dublin. Mr Barlee kindly sent me the specimens, which were *E. clausa*. Later he sent me another specimen from Kingstown which was more fully developed than any so far recorded. It had fifteen fully developed tentacular bulbs and seven smaller ones and its gonads were 1·2 mm. long and 0·65 mm. wide.

Helgicirrha schulzei Hartlaub.

In 1934 Künne drew attention to the distinction between *Eirene viridula** and Hartlaub's species *Helgicirrha schulzei*, which had been rather overlooked. Careful examination revealed the fact that *Helgicirrha* occurs off Plymouth. I had not realized the existence of this species until I saw Künne's paper, and my records for the species only date from 1935. A few specimens were found in each of the years 1935–7, and they occur in the plankton in the months of June to October inclusive. Its seasonal distribution thus overlaps that of *Eirene*, which reaches its maximum abundance in September and October, and the two species are likely to be found together. A re-examination of samples for the years previous to 1935 showed that the great majority of the specimens identified as *E. viridula* were correct. An occasional specimen of *Helgicirrha* was, however, found, but it is quite certain that they were too few to affect the general picture of the seasonal distribution of *Eirene* given in Table III.

---

* No attempt has been made in this report to distinguish *E. viridula* and *E. pellucida* on the preserved material; they are possibly the same species.

In living specimens of *Helgicirrha schulzei* there are fine specks of deep indigo pigment all round the extreme margin of the umbrella. This pigment was not present in living specimens of *Eirene pellucida*.

The genera *Eirene* and *Helgicirrha* have recently been revised by Kramp (1936). He pointed out that Hartlaub's spelling *schulzii* should be more correctly *schulzei*.

Aglantha rosea (Forbes).

In 1930 *Aglantha*, which always accompanies "*elegans*" water, was present off Plymouth throughout most of the year. The opportunity was taken to see whether size measurements would throw any light on the life history of this medusa. The umbrella height was accordingly measured on samples from each catch. In Fig. 5 a curve is given showing the actual numbers caught between February and October. The numbers were low until June when they began to increase very rapidly, reaching a maximum of many thousands in August. Curves are also given in Fig. 5 for the height measurements of the medusae on each date. From February to April the *Aglantha* were large, being 12–18 mm. in height. A new brood, presumably arising from these large individuals, appeared in April, and these medusae reached a size of 6–8 mm. in May. Thereafter reproduction was rapid and the production of successive generations probably overlaps. Nevertheless, the height measurements do appear to give some indication of successive generations. In Fig. 5 a large dot is placed on the base line opposite the highest peak for each curve. It can be seen that there are three definite series in June, July and August each one of which starts at a small size and shows a gradual increase to a maximum. Perhaps too much stress should not be laid on these until they can be repeated in another year, but the indications are that three successive generations arose in June, July and August, each taking about 1 month to grow up. In September there was a slight increase in the size of the medusae, and it is probable that these live through the winter to grow into the large individuals found in February.

The annual sequence thus seems to be as follows: The year starts with large individuals 12–18 mm. in height which were produced by the last spawning of the previous year. These large medusae spawn in late March and their offspring mature in May, after which there are three, or possibly four, successive generations produced in the summer. These summer medusae only grow to a height of about 5–7 mm. Five or six generations are thus produced in a year.

The large individuals found from February to April were strong and muscular, a characteristic of deep water medusae. Kramp (1927) records

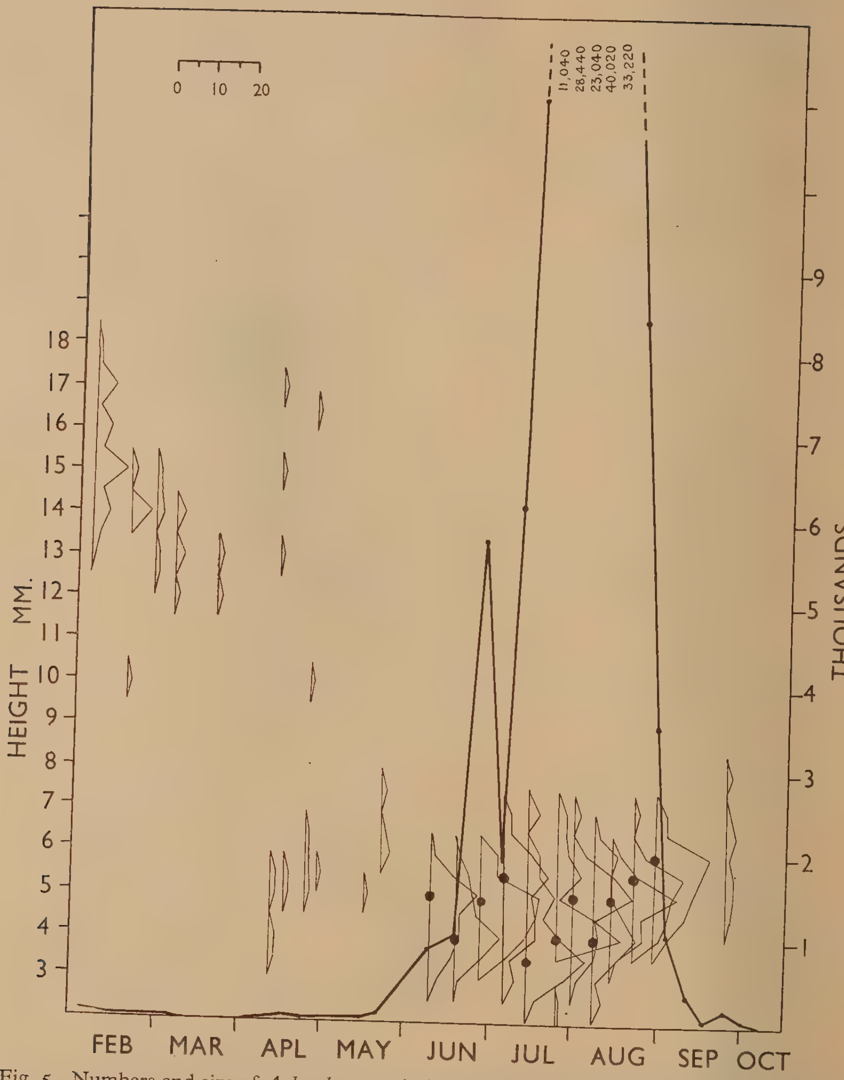


Fig. 5. Numbers and size of *Aglantha rosea* in half-hour oblique hauls with the 2 m. stramin ringtrawl off Plymouth in 1930. The thick curve gives the numbers caught in thousands; the small curves show the size distribution in each catch, the scale for numbers being in the top left-hand corner.

that two forms are to be found in Danish waters, one inhabiting the North Sea and upper water layers of the Skagerrak reaching a height of 16 mm. and a smaller form found in the Kattegat and Belt Sea hardly growing to more than 12 mm. in height. He makes the suggestion that it is the shallowness of the water that renders the Belt Sea unsuitable as a permanent habitat for *Aglantha*. It may well be that the large medusae found off Plymouth had come from deep water where they need to retire for the winter months, and that this necessity prevents them from becoming permanently established in the waters off Plymouth. Günther (1903) says concerning *A. rosea* off the west of Ireland: "It seems possible that fully developed *Aglantha* may live near the surface during the summer months, but may sink into deeper waters with the advancing season."

It is uncertain whether *A. rosea* should be regarded as a variety of *A. digitalis* or as a distinct species. The chief structural difference, apart from size, is that while in *A. digitalis* there are only four marginal sense organs, in *A. rosea* there are eight. In March 1936 I obtained some very young specimens of *A. rosea* off Plymouth and was able to examine them alive. Specimens up to just under 4 mm. in height, with twenty to thirty tentacles, had only four sense organs; a specimen 4·4 mm. in height with thirty-four tentacles had five sense organs, while specimens 5 and 6 mm. in height had eight. It is evident that the number of marginal sense organs increases from four to eight when the medusa is somewhere between 4 and 5 mm. high. Since *A. rosea* begins by developing four sense organs and not eight it is unnecessary to suppose that, if it is a variety, *A. digitalis* must have lost four sense organs during the course of its development. It must remain therefore a matter of opinion whether the two are to be regarded as varieties or distinct species on account of their different distribution and habits.

SUMMARY

The composition of the medusa fauna in offshore waters off Plymouth is reviewed. A table is given showing the months in which the different species have been recorded and those months in which they are most abundant.

A preliminary list has been drawn up attempting to discriminate between those species which are regularly indigenous off Plymouth and those which are brought from elsewhere by water movements.

The results of weekly hauls with the 2 m. stramin ringtrawl during the years 1930–7 inclusive are given. The years 1935, 1936 and 1937 have been noteworthy for the paucity of all species of medusae.

Observations on the structure and biology of certain species of medusae are recorded.

TABLE III. AVERAGE CATCHES FOR EACH MONTH IN THE YEARS 1930–7

Half-hour oblique hauls with 2 m. stramin ringtrawl

	Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Steenstrupia nutans	1930		..	..	..	..	20	24	2	..	..	..	..	46
	1931	..	..	..	..	110	13	..	..	..	..	..	..	123
	1932	..	..	..	..	10	54	..	..	..	..	..	..	64
	1933	..	..	..	15	2	..	1	..	..	..	..	..	18
	1934	..	..	..	13	1219	+	..	..	..	..	..	..	1232
	1935	..	..	..	..	6	..	..	..	..	..	..	..	6
	1936	..	..	..	+	4	11	+	..	..	..		..	15
	1937	..	..	..	..	37	22	..	..	..	..	..	..	59
Bougainvillia britannica	1930		..	..	..	157	107	32	..	..	..	..	..	296
	1931	..	..	..	6	9	97	..	..	..	..	..	..	112
	1932	..	..	..	..	155	247	..	..	..	..	..	..	402
	1933	..	..	..	+	4	..	..	..	..	..	..	..	4
	1934	..	..	..	63	1222	..	..	..	..	..	..	..	1285
	1935	..	..	..	..	33	..	..	..	..	..	..	1	34
	1936	..	..	..	..	1	1	..	..	..	..		..	2
	1937	..	..	..	+	1	1	..	..	..	..	..	..	2
Turritopsis nutricula	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	..	..	..	..	..	..
	1932	..	..	..	..	..	..	..	..	..	..	..	..	..
	1933	..	..	..	..	..	..	..	+	8	5	3	1	17
	1934	1	..	..	..	..	..	..	..	..	+*	+*	..	1
	1935	..	..	..	..	..	..	..	..	2	1	..	..	3
	1936	..	..	..	..	..	..	..	+	4	21		..	25
	1937	..	..	..	..	..	..	..	1	14	15	3	1	34
Amphinema dinema	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	..	..	..	..	..	..
	1932	..	..	..	..	..	..	..	..	..	6	..	..	6
	1933	..	..	..	..	..	..	..	..	1	4	3	..	8
	1934	..	..	..	..	..	..	..	..	1	6	..	..	7
	1935	..	..	..	..	..	..	..	..	11	96	..	..	107
	1936	+	..	..	..	..	..	..	..	11	44		..	55
	1937	..	..	..	..	..	..	..	..	48	22	+	..	70
Amphinema rugosum	1930		..	..	..	..	7	466	+	..	..	..	..	473
	1931	..	..	..	..	1	..	..	..	..	..	..	..	1
	1932	..	..	..	..	..	21	..	..	..	..	..	..	21
	1933	..	..	..	13	..	..	..	..	..	..	..	..	13
	1934	..	..	..	..	2	..	..	..	..	..	..	..	2
	1935	..	..	..	..	..	..	..	..	..	..	..	..	..
	1936	..	..	..	..	..	..	..	..	..	7		..	7
	1937	..	..	..	..	..	..	..	..	+	2	..	..	2
Leuckartiara octona	1930		..	..	1	47	296	164	81	61	5	3	..	658
	1931	..	5	6	12	77	173	63	63	90	24	..	+	513
	1932	..	..	3	8	100	133	55	30	62	10	1	1	403
	1933	..	+	1	25	59	104	7	4	16	2	+	..	218
	1934	..	..	..	1	66	23	4	4	..	10	..	..	108
	1935	..	..	..	+	48	39	6	3	2	4	..	..	102
	1936	..	..	+	..	6	60	2	..	+	..		..	68
	1937	..	..	1	1	2	9	+	1	1	1	..	..	16
Laodicea undulata	1930		..	..	2	10	10	..	1040	4079	..	..	..	5141
	1931	..	..	15	20	..	..	3	363	1944	182	..	..	2527
	1932	..	..	..	..	..	7	..	1	14	..	..	..	22
	1933	..	..	..	1	8	..	..	60	1	..	..	..	70
	1934	..	..	5	+	1	..	6	265	5	+	...	..	282
	1935	..	..	+	..	+	..	+	1	206	1	..	..	208
	1936	..	..	1	..	1	..	..	..	+	2		..	4
	1937	..	..	+	2	+	..	5	4	6	1	+	..	18
Cosmetira pilosella	1930		..	..	66	52	83	672	15	3	..	..	..	891
	1931	..	..	..	528	900	520	25	100	38	..	..	..	2111
	1932	..	..	..	70	1055	300	765	401	8	..	..	..	2599
	1933	..	..	..	93	12	220	1	..	..	..	..	..	326
	1934	..	..	3	11	328†	..	..	..	..	..	..	..	342
	1935	..	..	..	..	41	..	..	+	..	..	..	..	41
	1936	..	..	..	..	2	4	..	..	..	+		..	6
	1937	..	..	1	3	2	1	..	..	+	..	..	..	7
Obelia spp.	1930		..	..	..	573	455	14206	123	53	8	..	..	15418
	1931	..	..	35	..	449	7	60	760	..	..	..	..	1311
	1932	..	..	..	745	14040	3587	45	40	66	123	5	5	18656
	1933	5	..	48	1096	153	40	40	34	263	718	330	3	2730
	1934	2	+	9	2092	10788	393	13	87	8	85	170	2	13649
	1935	..	+	5	226	1176	10	43	10	108	356	..	1	1935
	1936	..	..	10	26	543	180	33	5	..	..		..	797
	1937	..	..	1	47	718	115	255	165	213	388	163	3	2068

* Seen in townet catches.

† I had in my notes a record for May 29 "many". I have given this number as 1000.

TABLE III (*cont.*)

Half-hour oblique hauls with 2 m. stramin ringtrawl.

	Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Phialidium hemisphericum	1930		..	..	68	415	510	3442	2855	1305	310	15	30	8950
	1931	20	30	3170	3006	1378	2807	1393	443	83	..	60	164	12554
	1932	10	..	5	133	1885	1247	510	80	1106	795	70	21	5862
	1933	69	54	67	1145	998	4000	2115	71	536	138	271	48	9512
	1934	18	2	131	508	4144	85	150	38	15	19	69	..	5179
	1935	3	6	7	53	89	18	148	28	135	92	1	20	600
	1936	32	29	6	2	253	148	52	5	29	392		+	948
	1937	..	..	116	13	267	124	88	48	591	1267	80	11	2605
Saphenia gracilis	1930		..	..	8	37	4	66	22	20	..	..	..	157
	1931	..	..	..	..	7	..	..	15	..	..	..	..	22
	1932	..	..	..	..	15	..	..	10	2	..	1	..	28
	1933	..	..	..	16	2	..	45	1	1	+	2	..	67
	1934	..	..	..	4	11	..	7	2	4	5	1	..	34
	1935	..	..	..	..	3	..	9	2	19	6	..	..	39
	1936	+	+	+	8	17	65	42	2	2	..		..	136
	1937	..	..	+	9	40	29	14	7	8	1	..	..	108
Octorchis gegenbauri	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	15	8	5	..	..	28
	1932	..	..	..	..	..	..	..	..	..	+	..	..	+
	1933	..	..	..	..	..	..	2	5	1	..	..	..	8
	1934	+	..	..	..	..	..	8	..	..	2	..	..	10
	1935	..	..	..	..	..	..	3	28	4	1	..	..	36
	1936	..	..	..	..	..	..	..	..	8	6		..	14
	1937	..	..	..	..	..	..	1	13	11	..	..	..	25
Eirene viridula	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	5	608	701	..	..	1314
	1932	..	..	..	..	..	..	..	1	70	6	3	3	83
	1933	..	..	..	..	..	..	..	+	34	11	10	1	56
	1934	..	..	..	..	..	..	1	..	..	+	..	..	1
	1935	..	..	..	..	..	..	..	1	4	2	..	..	7
	1936	..	..	..	..	..	..	..	..	..	2		..	2
	1937	..	..	..	..	..	..	..	1	14	23	1	..	39
Helgicirrha schulzei	1935	..	..	..	..	..	..	+	..	2	1	..	..	3
	1936	..	..	..	..	..	2	+	+	+	..		..	2
	1937	..	..	..	..	..	..	..	1	..	..	..	..	1
Aequorea forskalea	1930		..	..	..	..	..	+	+	..	..	..	..	+
	1931	..	..	..	1	..	..	..	1	7	3	1	..	13
	1932	..	..	..	..	..	..	..	+	1	1	1	1	4
	1933	..	..	..	..	..	..	..	..	..	..	..	..	..
	1934	..	..	..	..	..	..	..	..	..	+	..	..	+
	1935	..	..	1	..	..	..	..	..	..	+	..	..	1
	1936	..	..	..	..	+	2	..	..	..	..		..	2
	1937	..	..	..	..	..	..	..	+	+	+	..	..	+
Gossea corynetes	1930		..	..	..	..	..	..	..	..	..	..	..	..
	1931	..	..	..	..	..	..	..	..	4	8	..	..	12
	1932	..	..	..	..	..	..	..	..	+	1	..	..	1
	1933	..	..	..	..	..	..	1	1	2	+	..	..	4
	1934	..	..	..	..	..	..	..	8	1	1	1	..	11
	1935	..	..	..	..	..	..	..	..	5	1	..	..	6
	1936	..	..	..	..	..	..	..	..	1	..		..	1
	1937	..	..	..	..	..	..	1	11	1	..	..	..	13
Aglantha rosea	1930		17	2	9	43	2529	14120	21285	413	18	3	..	38439
	1931	..	..	..	..	..	..	128	15	+	..	..	..	143
	1932	..	..	..	..	..	..	..	..	..	..	..	..	..
	1933	..	..	..	1	..	..	..	..	..	..	..	..	1
	1934	..	..	..	..	..	..	..	3	4	22	2	1	32
	1935	+	..	..	..	+	..	21	1	..	+	..	..	22
	1936	..	..	6	+	9	93	201	116	..	..		..	425
	1937	..	1	+	+	3	27	29	..	..	..	..	..	60
Liriope exigua	1930		..	..	..	1	+	+	6332	5610	1655	1183	741	15522
	1931	325	1	..	..	..	..	..	..	..	1	..	..	327
	1932	..	..	..	..	..	..	..	..	..	..	..	..	..
	1933	..	..	..	..	..	..	..	..	..	+	3	+	3
	1934	+	..	..	..	..	..	..	..	..	..	..	..	+
	1935	+	..	..	..	..	..	..	..	..	..	..	..	+
	1936	..	..	..	..	..	..	..	..	..	..		..	..
	1937	..	..	..	..	..	..	..	..	..	..	..	..	..

REFERENCES

Bigelow, Henry B., 1913. Medusae and Siphonophorae collected by the U.S. Fisheries Steamer "Albatross" in the Northwestern Pacific, 1906. *Proc. U.S. Nat. Mus.*, Vol. 44, No. 1946, pp. 1–119.

Browne, Edward T., 1896. On British Hydroids and Medusae. *Proc. Zool. Soc.* London, pp. 459–500.

— 1898. On the pelagic fauna of Plymouth for September, 1897. *Journ. Mar. Biol. Assoc.*, Vol. v, pp. 186–92.

— 1900. The fauna and flora of Valencia Harbour on the west coast of Ireland. II. The Medusae (1895–98). *Proc. Roy. Irish Acad.*, 3rd Ser., Vol. v, No. 5, pp. 694–736.

— 1902. A Preliminary Report on Hydromedusae from the Falkland Islands. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. ix, pp. 272–84.

— 1906. Biscayan plankton collected during a cruise of H.M.S. "Research", 1900. Part IX. The Medusae. *Trans. Linn. Soc. (Zool.) London*, 2nd ser. Vol. x, Pt 6, pp. 163–87.

— 1910. Coelentera. V. Medusae. *National Antarct. Exped.* 1901–1904, *Nat. Hist.*, Vol. v, Zool. and Bot., pp. 1–62.

Carruthers, J. N., 1934. The flow of water past the Seven Stones Lightvessel. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 921–30.

Delap, M. and C., 1905. Notes on the plankton of Valencia Harbour, 1899–1901. *Ann. Rep. Fish. Ireland*, 1902–03, Pt. ii, App. i [1905], pp. 1–19.

— 1906. Notes on the plankton of Valencia Harbour. *Fisheries, Ireland, Sci. Invest.*, 1905, No. vii, pp. 3–21.

Foerster, R. Earle, 1923. The Hydromedusae of the west coast of North America, with special reference to those of the Vancouver Island Region. *Contr. Canad. Biol.* N.S., Vol. i, No. 12, pp. 221–77.

Forbes, Edward, 1848. A Monograph of the British Naked-eyed Medusae. *Ray Society.*

Garstang, Walter, 1894. Faunistic notes at Plymouth during 1893–4. *Journ. Mar. Biol. Assoc.*, Vol. iii, pp. 210–35.

Günther, R. T. 1903. Report on the Coelenterata from the intermediate waters of the N. Atlantic, obtained by Mr George Murray during the Cruise of the "Oceana" in 1898. *Ann. Mag. Nat. Hist.*, Ser. 7, Vol. xi, pp. 420–30.

Hartlaub, C., 1909. Über *Thaumantias pilosella* Forbes und die neue Lafoëiden-Gattung *Cosmetira*. *Zool. Anz.*, Bd. xxxiv, Nr. 3/4, I. Wiss. Mitt. 2, pp. 82–9.

— 1911. Craspedote Medusen, Teil I, Lief. 2, Margelidae. *Nordisches Plankton*, Lief. 15, xii, pp. 137–235.

— 1917. Craspedote Medusen. Teil I, Lief. 4. *Nordisches Plankton*, Lief. 19, xii, pp. 365–479.

Kramp, P. L., 1927. The Hydromedusae of the Danish Waters. *D. Kgl. Danske Vidensk. Selsk. Skr., Naturvid. Math.*, Afd. 8, Raekke xii, No. 1, pp. 1–291.

— 1930. Hydromedusae collected in the south-western part of the North Sea and in the eastern part of the Channel in 1903–1914. *Mém. Mus. Roy. Hist. Nat. Belgique*, Mem. No. 45, pp. 1–55.

— 1933. Craspedote Medusen. Teil 3, Leptomedusen. *Nordisches Plankton*, Lief. 22, xii, pp. 541–602.

— 1936. On the Leptomedusae of the Genera *Eirene* Eschscholtz and *Helgicirrha* Hartlaub. *Vidensk. Medd. Dansk. Naturh. Foren.*, Bd. 99, pp. 239–62.

Künne, Cl., 1934. Über die Leptomedusen *Helgicirrha schulzii* Hartlaub und *Eirene viridula* (Péron und Lesueur). *Zool. Anz.*, Bd. 106, Heft 1/2, pp. 27–34.

Künne, Cl., 1937. Über die Verbreitung der Leitformen des Grossplanktons in der südlichen Nordsee im Winter. *Ber. Deutsche Wiss. Komm. Meeresforsch.*, Berlin, N.F., Bd. viii, Heft 3, pp. 131–64.

Mayer, Alfred Goldsborough, 1910. *Medusae of the World*, Vol. i, pp. 1–230.

Orton, J. H., 1920. Sea-temperature, breeding and distribution in marine animals. *Journ. Mar. Biol. Assoc.*, Vol. xii, pp. 339–66.

Rees, W. J. & Russell, F. S., 1937. On rearing the hydroids of certain medusae, with an account of the methods used. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 61–82.

Russell, F. S., 1933. The seasonal distribution of macroplankton as shown by catches in the 2-metre stramin ring-trawl in offshore waters off Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xix, pp. 73–82.

— 1930–8. The seasonal abundance and distribution of the pelagic young of Teleostean fishes caught in the ring-trawl in offshore waters in the Plymouth area. I–V. *Journ. Mar. Biol. Assoc.*, Vols. xvi, p. 707; xx, pp. 147 and 595; xxi, p. 679; xxii, pp. 493–500.

— 1936 *a*. The importance of certain plankton animals as indicators of water movements in the western end of the English Channel. *Rapp. Proc. Verb. Int. Cons. Explor. Mer*, Vol. c, pp. 7–10.

— 1936 *b*. On a new species of medusa, *Eucheilota hartlaubi* n.sp. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 589–94.

— 1936 *c*. On the first stage of the medusa *Eucheilota clausa* (Hincks) [=*E. hartlaubi* Russell]. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 131–3.

Russell, F. S., & Rees, W. J., 1936. On rearing the hydroid *Zanclea implexa* (Alder) and its medusa *Zanclea gemmosa* McCrady, with a review of the genus *Zanclea*. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 107–130.

Thiel, Max Egon, 1932. Die Hydromedusen-fauna des Nördlichen Eismeeres in tiergeographischer Betrachtung. *Arch. Naturgesch.* Berlin, Abt. B, N.F., Bd. 1, Heft 3, pp. 435–514.

Wulff, A., Bückmann, A., & Künne, Cl., 1934. Bericht über die Teilnahme an einer Fischereischutzfahrt der "Weser" zu Untersuchungen über die Verbreitung der Heringslarven in der Südlichen Nordsee und dem Kanaleingang. 7 November bis 15 December 1933. *Ber. Deutsche Wiss. Komm. Meeresforch.*, Berlin, N.F., Bd. vii, Heft 3, pp. 328–42.

ON THE DEVELOPMENT OF *MUGGIAEA ATLANTICA* CUNNINGHAM

By F. S. Russell, B.A., F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–6)

In September 1937 *Muggiaea atlantica* Cunningham was very abundant off Plymouth. The presence of large numbers of eudoxids in the plankton afforded an opportunity to rear the early stages of this siphonophore. The development of *M. kochi* (Will) was worked out by Chun (1882, 1913), and he also described the eudoxid of that species. The eudoxid of *M. atlantica* has, however, never been described for certain. The allocation of eudoxids collected in the plankton to their respective species is necessarily fraught with uncertainty when more than one species is present. Throughout the whole of September 1937 *M. atlantica* was the only species of siphonophore to be found off Plymouth, and there can be no reasonable doubt that the eudoxids described below belonged to that species and that the development of the early stages from their eggs is that of *M. atlantica*.

For the terminology used in the description of the eudoxid I have followed Totton (1932), to whom I am grateful for helpful advice.

THE EUDOXID

The *bract* (Fig. 2 *a*) is cone-shaped with a broad flat suture running from its apex to the base. The edges of the suture are raised into a slight flange. The right edge is continued downwards into a sweeping curve while the left edge cuts away horizontally at its lower end; the bract is thus asymmetrical. There is a slight cavity on the lower surface in which the somatocyst is centrally placed. The general form of the bract can also be seen in the different views of the whole eudoxid given in Fig. 1. The largest bract seen had an overall height of 1·9 mm.

The *gonophore* bell (Fig. 1) is cylindrical and has four longitudinal ridges running from the apex to the velar opening with a spiral twist to the right. The two ventral ridges are prolonged below the velar opening and join to form a short curved mouth-plate. The right ventral ridge is more strongly developed than any of the others (Fig. 2 *b*). Specimens with left-handed twisting, or "mirror images", are common (Fig. 2 *c*) and are presumably the second gonophores to be budded. The edges of the ridges are quite smooth, although some may show very faint traces of irregularity. The manubrium in fully developed gonophores extends more than two-thirds the length of the subumbrella cavity and has a pink tip. The radial canals follow the spiral courses of the ridges.

The height of the whole eudoxid is usually about 2–2·5 mm.; isolated gonophore bells have been found up to 2·2 mm. in height. One eudoxid was seen with twenty-one nematocyst batteries on its tentacle.

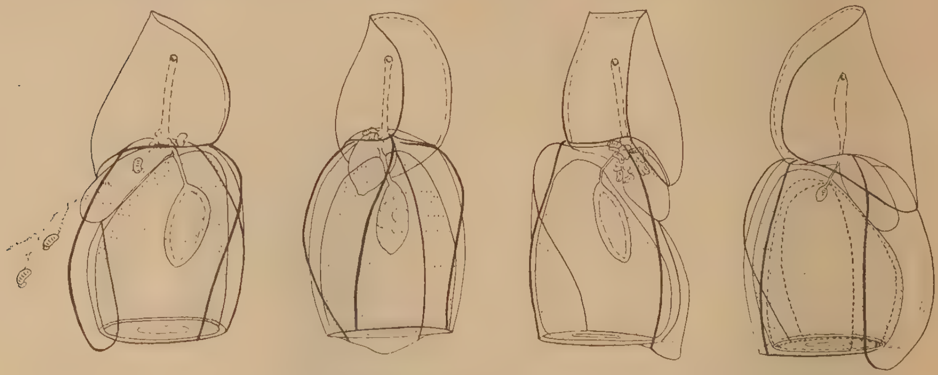


Fig. 1. Different views of eudoxids of *Muggiaea atlantica*, Plymouth, Sept. 1937. Height of original specimens from left to right 2·5, 2·5, 2·4 (bract somewhat twisted above gonophore) and 1·8 mm.

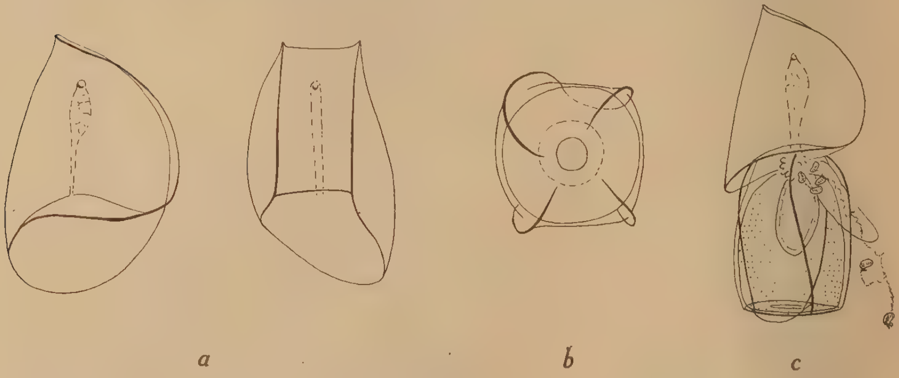


Fig. 2. Eudoxid of *Muggiaea atlantica*, Plymouth, Sept. 1937. *a*, lateral and ventral views of bract; overall height 1·7 mm.; *b*, apical view of gonophore; the ventral side is uppermost; *c*, eudoxid with "mirror image" gonophore; total height 2·2 mm.

The figures given here are drawings of living specimens; when preserved the gonophore bell appears much more angular and the ridges are more prominent owing to the contraction of the bell. In many dead or dying gonophores the apex showed the inflated condition figured by Totton (1932, fig. 33 *B*) for *Lensia subtiloides*.

No essential difference can be seen between my figures and the drawing given by Chun (1882) of the eudoxid of *Muggiaea kochi*. The only difference in Moser's (1925) account of the eudoxid of *M. kochi* is that the gonophore bell is laterally flattened; this, however, is probably an effect of preservation.

As already stated the circumstances under which my eudoxids were obtained practically remove all doubt that they belong to *M. atlantica*. Since for some years previous to 1936 *M. kochi* completely took the place of *M. atlantica* off Plymouth (Russell, 1934), I have been able to refer to previous collections. Some eudoxids were found with a sample of *M. kochi* taken on October 12 1933. When these were placed beside eudoxids of *M. atlantica* caught this year no differences could be detected, and we must conclude that the eudoxids of the two species are probably indistinguishable, at any rate in their grosser features.

THE EARLY DEVELOPMENT

A number of successful fertilizations from the eudoxids of *M. atlantica* were made in the Laboratory in September 1937, and the development was observed until the first appearance of the secondary nectophore.

The eggs are transparent, 0·25 mm. in diameter, and float near the surface of the water. Segmentation is regular, a spherical ciliated embryo being formed 0·27 mm. in diameter; this quickly becomes pear-shaped and within 24 hours develops into a typical elongated planula *ca.* 0·37 mm. in length. The rudiments of the primary nectophore soon appear as slight bulges on one side of the planula and proliferation of the posterior cells to form the siphon takes place. At this stage there is a pinkish tinge along that side on which development occurs. In less than 36 hr. the cavity of the primary nectophore is already formed and the somatocyst appearing (Fig. 3). Within 48 hr. the nectophore is fully formed (Fig. 3) and pulsating. The whole larva, umbrella included, is ciliated, so that when not moving by pulsation it rotates slowly by ciliary action. A cushion develops on the exumbrella on either side of the remains of the planula and a hydroecial groove is formed. By the next day all signs of the original tissue of the planula have disappeared and the primary nectophore is fully developed with somatocyst, siphon, tentacle with seven or eight nematocyst batteries and the rudiments of the secondary nectophore. Figs. 3, 4 show the course of development of specimens reared in the laboratory from the planula to the fully developed primary nectophore. The latest stage there shown is apparently abnormal, for specimens taken from the plankton at the same stage of development were larger and much higher (Fig. 5). In those from the plankton there was also an oil globule in the somatocyst showing that the animals had fed. The laboratory reared specimens were not fed and later development has probably taken place at the expense of the tissues, resulting in abnormal shape in the bell. After examination of a number of specimens from the plankton ranging between 0·9 and 1·3 mm. in height it

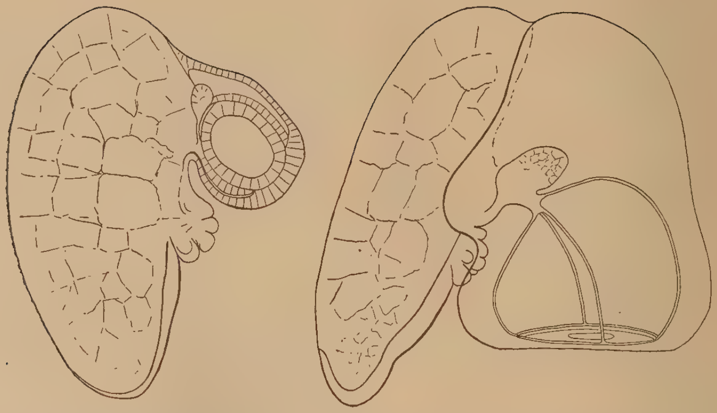


Fig. 3. Developing embryos of *Muggiaea atlantica* reared in the laboratory at Plymouth, Sept. 1937. Left, *ca.* 36 hr. old, length of planula 0·37 mm. Right, less than 48 hr. old, umbrella height 0·38 mm.

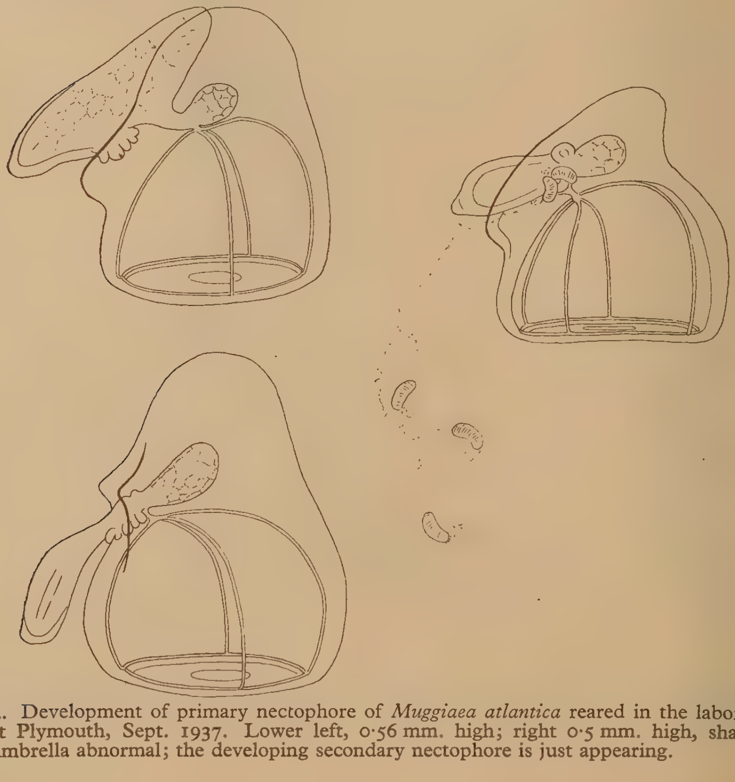


Fig. 4. Development of primary nectophore of *Muggiaea atlantica* reared in the laboratory at Plymouth, Sept. 1937. Lower left, 0·56 mm. high; right 0·5 mm. high, shape of umbrella abnormal; the developing secondary nectophore is just appearing.

appears that the normal shape is that shown in Fig. 5, though an occasional specimen more like that reared in the laboratory was found.

No specimens were seen in which the primary and fully developed secondary nectophores were both present together. But very small secondary nectophores were found with the remains of their attachment to the primary nectophore still present (Fig. 6), and many cast primary nectophores were also seen loose in the plankton. In the smallest secondary nectophore, which was 0·4 mm. in height, the somatocyst already extended to the top of the subumbrella cavity and the species could thus be identified as *M. atlantica*.

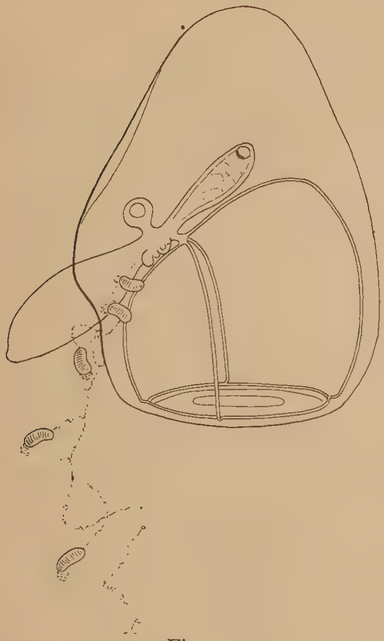


Fig. 5.

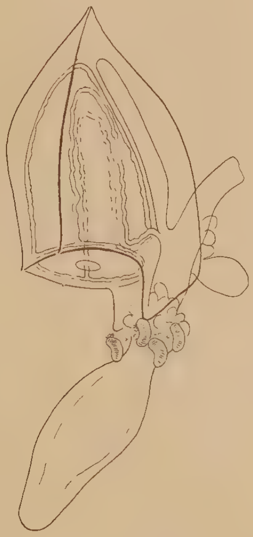


Fig. 6.

Fig. 5. Primary nectophore of *Muggiaea atlantica* 1·3 mm. high, normal shape, from plankton, Plymouth, Sept. 1937.

Fig. 6. Secondary nectophore of *Muggiaea atlantica* recently separated from primary nectophore; height from apex to velar opening 0·67 mm., from plankton, Plymouth, Sept. 1937.

The course of development here outlined agrees with that given by Chun (1882) for *M. kochi*. The normal shape of the primary bell of *M. atlantica* differs from Chun's drawing of that of *M. kochi* in that the apical process is more dome shaped. In view of the variability of this character it is not certain whether Chun's figure is that of a normal specimen and it is possible that the two species would be hardly distinguishable at this stage unless it be in the microscopic structure of the nematocyst batteries. Once the secondary nectophore is developed, however, the two species become at once recognizable by the difference in the lengths of the somatocyst, that in *M. kochi* being much the shorter.

REFERENCES

Chun, Carl, 1882. Über die cyklische Entwickelung und die Verwandtschaftsverhältnisse der Siphonophoren. *Sitz. König. Preuss. Akad. Wiss. Berlin*, Phys.-Math. Kl., Bd. LII, pp. 1155–72.

— 1913. Über den Wechsel der Glocken bei Siphonophoren. *Ber. Verh. König. Sächs. Ges. Wiss. Leipzig*, Math.-Phys. Kl., Bd. LXV, pp. 27–41.

Moser, F., 1925. Die Siphonophoren der Deutschen Südpolar-Expedition 1901–1903, zugleich eine neue Darstellung der ontogenetischen und phylogenetischen Entwickelung dieser Klasse. *Deutsche Südpolar-Exped.*, Bd. XVII, Zoologie, Bd. IX, pp. 1–541.

Russell, F. S., 1934. On the occurrence of the siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochi* (Will) in the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 555–8.

Totton, A. K., 1932. Siphonophora. *Great Barrier Reef Exp.* 1928–29. *Sci. Rep.*, Vol. IV, No. 10, pp. 317–74, Brit. Mus. (Nat. Hist.).

THE LIFE HISTORY OF *KELLIA SUBORBICULARIS*

By Marie V. Lebour, D.Sc.
Naturalist at the Plymouth Laboratory

(Text-fig. 1)

Kellia suborbicularis (Montagu) has long been known to be viviparous. Lovén (1848) mentions this fact and Jeffreys (1863, p. 227) quotes Mr Clark who "found in the ovary of one individual ova in an advanced state with fully formed testaceous fry". It is probable, however, that these shelled larvae were in reality contained in the gill pouch where later workers have found them. Pelseneer (1935, p. 517) says that the eggs are incubated in the internal gill lamella, and this was also observed by myself.

It is striking that although the shelled larva is extremely small when liberated (shell 0·064–0·08 mm. in length), the late planktonic larva is very large (shell 0·30–0·37 mm. in length) and one of the most conspicuous bivalve veligers in the plankton. This indicates a prolonged free-swimming life quite unlike that of the oyster, *Ostraea edulis*, whose shelled larvae are liberated only to lose the velum in a few days. These late larvae of *Kellia* have been kept in bowls and plunger jars in the Plymouth Laboratory until they metamorphosed and for months afterwards, growing into beautifully clear and transparent individuals which undoubtedly belonged to this species.

Kellia suborbicularis is placed by Winckworth (1932) in the Erycinidae, but this family is closely related to the Leptonidae, Montacutidae and Galeommatidae, most or all of whose members are viviparous. Lovén (1848) described the young shelled stage of *Montacuta ferruginosa* and *M. bidentata*, the latter species now being referred by Winckworth to *Mysella*. Both keep their young in the gill pouch until the shelled stage and Lovén's beautiful figures show that the early shelled stage in each of them is very like that of *Kellia*. Both, however, are larger when ejected and more developed (*M. ferruginosa* 0·14 mm. long, *M. bidentata* 0·15 mm. long, *Kellia suborbicularis* 0·064–0·08 mm. long). After being fed on flagellates *Kellia* at 0·12 mm. had developed further, although smaller than either of the others. The shape of the newly ejected shell is similar in all three. *Kellia* grows rounder as it develops. The later stages of the other two are not known; but certain large veligers in the Plymouth plankton, now being investigated, seem to belong to *Mysella bidentata*, and if this is proved to be the truth we have another species, similar to *Kellia*, in which there is much growth in the free-swimming stage before metamorphosis.

When we realize that Lovén's work is now ninety years old it is somewhat astonishing that so little has been added to our knowledge of these most interesting larvae. *Lasaea rubra* incubates its eggs until a very late stage. *Galeomma turtoni* gave out embryos during the night of September 13 1937, which were in a much less advanced state than those of *Kellia*, having no shell although moving freely, the round embryo measuring 0·07 mm. across (these facts were kindly communicated by Miss Popham who is working at the group). A young *Turtonia minuta*, belonging to the same family as *Kellia*, grown in a plunger jar but in which the free-swimming stage was not noted, measured only 0·64 mm. in length and was just like the adult.

Kellia suborbicularis is fairly abundant at Plymouth on rocky shores in crevices and in dead shells and is also frequently dredged from deeper water in the Sound and outside, especially from the Stoke Point Grounds in crevices of red rock or in empty burrowing shells. Developing eggs were found in the gill pouches in May, July and August, but no eggs were seen in the winter months although several specimens contained active sperm in October. Shelled larvae were given off in September and October. Late larvae are present in the plankton in any month of the year both inside and outside the Sound, but especially in summer and early autumn. At this time they are some of the most conspicuous bivalve veligers, occurring with others of about the same size (*Lima*, *Saxicava* and, possibly, *Montacuta*). The breeding season appears to be spring, summer and early autumn with occasional larvae in winter.

Odhner (1914) found *Kellia suborbicularis* ripe in April at Rovigno, but does not mention the young in the gills. He notes the benthonic young in May with almost circular form, diameter (=length) 0·31 mm.; having a violet streak below the middle of the umbo and a greenish liver, and later stages with a red-brown pigment fleck under the adductors. It is at about this size that the larvae begin to lose the velum at Plymouth, but the violet streak and red spot were not noticed although there is frequently a red colour just inside the mantle edge.

The smallest developing egg seen from the gill pouch measured 0·025 mm. across and had divided into two segments; but in the same brood there were many celled spherical embryos 0·05 mm. across. On September 14 1937 Miss Popham found newly extruded larvae which had hatched out in a bowl during the night. Another brood was given out on October 11–12 during the night. Those from the September brood were very numerous and were swimming actively. The oval shell (Fig. 1 *a*, *b*) was perfectly transparent, smooth and colourless, the hinge line nearly straight, the length 0·064 mm. The organs were only feebly differentiated; but the velum, which was nearly half the length of the shell, was a fairly strong swimming organ surrounded by long and powerful cilia. A long and stronger cilium (the flagellum) was situated in the centre of the velum. The velar muscles were strongly developed.

The larvae given out in October were slightly larger and more developed

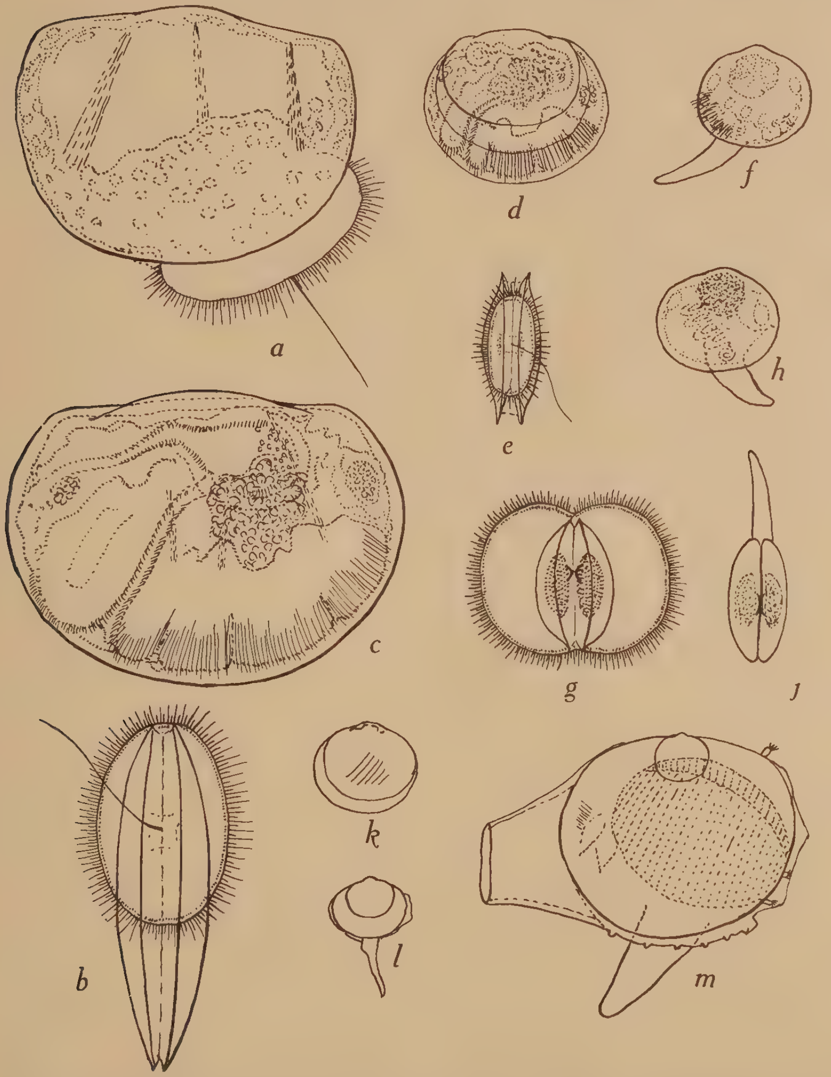


Fig. 1. *a*, veliger of *Kellia suborbicularis* newly extruded from parent's pouch, 0·064 mm. long, lateral view, September; *b*, the same, ventral view, swimming; *c*, veliger one day after extrusion, 0·08 mm. long, lateral view, October; *d*, veliger reared in plunger jar, extruded by parent in October, 14 days old, lateral view, 0·16 mm. long; *e*, the same, ventral view, swimming; *f*, late veliger from plankton, lateral view, 0·36 mm. long; *g*, the same, swimming, ventral view; *h*, newly metamorphosed larva, lateral view, 0·37 mm. long; *j*, the same, dorsal view; *k*, young shell, reared from planktonic veliger, 0·32 mm. long; *l*, slightly older shell, reared from planktonic veliger, 0·48 mm. long; *m*, older shell reared from planktonic veliger, 1·2 mm. long

than the September brood. These were placed in a plunger jar and given very small flagellates as food. On the morning of October 13, being one day old, they were swimming freely and feeding. The larva (Fig. 1 *c*) measured 0·08 mm. in shell length. The stomach, mouth and intestine were developed and were strongly ciliated, the stomach being full of flagellates. The liver was beginning to appear as a roundish mass at the side of and below the stomach. The anterior adductor muscle was fairly well developed, the posterior just beginning to appear below the end of the intestine. The velar muscles could still be seen, although hidden to a certain extent by the developing organs, and the velum was considerably larger. These larvae grew slowly but were active and fed well, the food being renewed every few days. When 14 days old they measured 0·11 mm. in shell length and 0·08 mm. in depth. The liver and stomach were turning a pale yellow, the stomach still being full of the flagellate food; the intestine was becoming twisted and the posterior adductor muscle was larger. The velum had increased in size and was held more centrally than in the very early larva, the flagellum being still conspicuous. At 3 weeks old the largest larva (Fig. 1 *d*, *e*) measured 0·16 mm. in shell length, but some were much smaller. At this point they ceased to grow, although still active and feeding, and they lived for a further 6 weeks. The larva at this size is very like the smallest recognized in the plankton; it has gradually grown from an oval to a round shape, the velum growing larger until it projects well beyond the shell.

It is probable that growth in the plunger jar is much slower than it is in nature, although the larva probably stays for a considerable time in the plankton in order to attain such a large size before metamorphosis. Veligers about 0·20 mm. in shell length may be recognized in the plankton and these are very similar to the largest reared in the plunger jar. They are, however, at this stage not very easy to differentiate from other species. The late larvae are easily recognizable. The largest veliger (Fig. 1 *f*, *g*) was 0·37 mm. in shell length, slightly less in breadth, and nearly spherical. From a shell length of 0·30–0·37 mm. the larva is ready to metamorphose. It has a faint yellowish tinge with touches of red irregularly present and is sometimes red all round the inside of the mantle margin. The general effect is colourless. The digestive gland is very conspicuous, forming two large greenish grey masses on each side just below the umbo. There are two to four gill slits, well-formed adductor muscles and a long contractile foot. The velum is very large and is slightly divided centrally at the anterior and posterior ends, the beginning of a bilobed structure usual in gastropods but very rare in bivalves. The velum is surrounded by powerful cilia and has lost the central flagellum; the whole organ projects far beyond the shell on each side. At this stage the animal can either crawl or swim and is now ready to metamorphose. The umbos of the shell are peculiarly prominent. The velum is now lost and the animal descends to the bottom.

These late veligers rapidly metamorphosed in plunger jars (Fig. 1 *h*, *j*) and the shell put on growth all round (Fig. 1*k*, *l*); the gills increased quickly and the mantle began to close up, showing the typical anterior and posterior siphons, the foot projecting from a central opening. At a length of 1·2 mm. the shell and animal are those of a typical *Kellia*, the embryonic shell still showing conspicuously at the apex (Fig. 1*m*). One specimen, kept for 6 months, measured 3·25 mm. in length and except for the absence of reproductive organs was in every way like the adult. Here again growth is probably slow, compared with that in natural surroundings, and it seems likely that the shell grows to its full size in a year. One female collected in August contained developing embryos and measured only 4 mm. in length, the largest being about 9 mm.

Newly metamorphosed *Kellia* were frequently found crawling on and in the red rock dredged from the Stoke Point Grounds. The smallest had a length of 0·32 mm. and intermediate stages between these and adults also occurred frequently; all were exactly similar to those reared in the plunger jars.

It seems certain that the young enter the holes and empty shells at a very early stage—a fact already noted by Montagu (1863, p. 39) who first described the species and stated that "it is to be found in holes in limestone the entrance being much smaller than the shell so that it must have entered in a young state".

It is thus established that *Kellia suborbicularis*, although it incubates its eggs until the larvae have formed a shell, must none the less remain in the plankton for a long time. It possesses a late veliger which is one of the largest planktonic bivalve larvae seen, and as the larvae are large and very numerous and occur practically throughout the year they must be important economically. The adult *Kellia* is known to form part of the food of the haddock (Jeffreys, 1863, p. 227).

REFERENCES

Jeffreys, J. G., 1863. *British Conchology*, Vol. II, pp. 1–464.

Lovén, S., 1848. Beiträge zur Kenntniss der Entwicklung der Mollusca Acephala Lamellibranchiata. *Abhandl. K. Schwed. Ak. Wiss.*, 1848. (Republished in 1879 at Stockholm with additional notes, pp. 1–39.)

Montagu, G., 1863. *Testacea Britannica*, pp. 1–606.

Odhner, N. H., 1914. Notizen über die Fauna der Adria bei Rovigno. Beiträge zur Kenntniss der marinen Molluskenfauna von Rovigno in Istrien. *Zool. Anz.*, Bd. XLIV, 4, pp. 156–70.

Pelseneer, P., 1935. Essai d'ethologie zoologique des Mollusques. *Acad. Roy. Belgique Cl. Sci.* Publications de la Fondation Agathen de Potter, No. 1, pp. 1–662.

Winckworth, R., 1932. The British Marine Mollusca. *Journ. Conch.*, Vol. 19, No. 7, pp. 211–52.

EVOLUTION OF CILIARY FEEDING IN THE PROSOBRANCHIA, WITH AN ACCOUNT OF FEEDING IN *CAPULUS UNGARICUS*

By C. M. Yonge, D.Sc.
University of Bristol

(Text-figs. 1–6)

CONTENTS

	PAGE
Introduction	453
Rejection Currents in the Mantle Cavity of the Prosobranchia	453
Evolution of Ciliary Feeding	455
Vermetus novae-hollandiae	456
Crepidula fornicata and other Calyptraeidae	457
Capulus ungaricus	459
Modification of gill filaments	461
Discussion	465
Summary	467
References	468

INTRODUCTION

Ciliary feeding, of such widespread occurrence in the Lamellibranchia, is confined in the Gastropoda to a few scattered groups. In freshwater Pulmonata, such as *Limnaea*, cilia on the foot assist in feeding when the animal is creeping suspended from the surface film (Brockmeier, 1898). Thecosomatous Pteropoda feed exclusively by the aid of cilia on the unpaired middle lobe and the paired side lobes of the foot, and an evolutionary series—*Cavolinia-Cymbulia-Gleba*—can be traced in which there is a progressive elaboration in the perfection of this mechanism and an accompanying reduction in the buccal mass and associated structures handed down from carnivorous ancestors (Yonge, 1926). Only in the few prosobranchs which have acquired ciliary feeding mechanisms do these represent a modification of the ctenidia as in the Lamellibranchia. They also, as it is the aim of this paper to show, represent a modification of the rejection currents present in the mantle cavity of typical prosobranchs.

REJECTION CURRENTS IN THE MANTLE CAVITY OF THE PROSOBRANCHIA

In typical Prosobranchia a respiratory current, created by the beating of the lateral cilia on the gill filaments, is drawn into the mantle cavity by way of the inhalent opening (frequently prolonged into a siphon, e.g. in *Buccinum*) on the left side of the head and, after passing between the gill filaments where respiration takes place, passes out by the exhalent opening on the right side. Any sediment present in the water must inevitably be drawn in with this current and, if the gills and other important organs in the mantle cavity are not to be smothered by it, it is essential that mechanisms should exist for its rapid and efficient removal. In a recent paper on *Aporrhais* (Yonge, 1937) it was shown that disposal of suspended matter is brought about by the following three well-defined sets of ciliary currents:

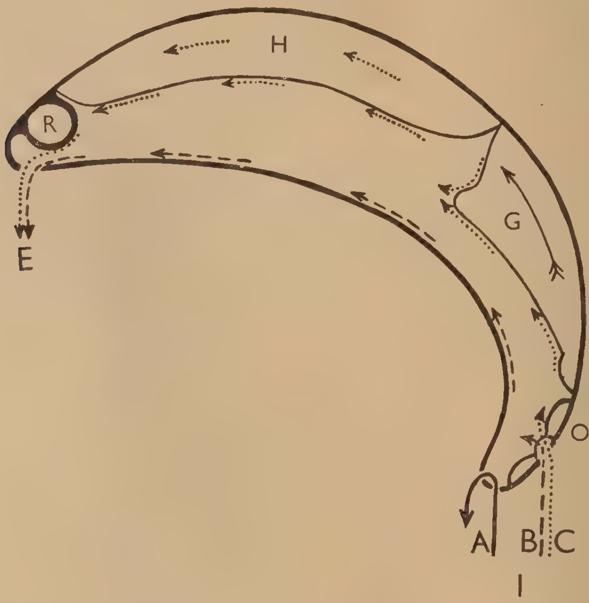


Fig. 1. Semi-diagrammatic representation of course of the ciliary currents within the mantle cavity of a typical pectinibranch prosobranch. A, B, C, three sets of rejection currents represented by unbroken, broken and dotted arrows respectively; E, exhalent current (downward arrows representing outward current at right angles to plane of figure); I, inhalent current (upward arrows representing inward current as before); G, gill filament (feathered arrow representing respiratory current created by lateral cilia); H, leaflet of hypobranchial gland; O, osphradium (with paired lateral plates as in *Buccinum*); R, rectum.

A. Cilia on the margin of the inhalent region carry the largest and heaviest particles, which tend to settle almost at once, directly to the exterior, i.e. by way of the inhalent opening.

B. Cilia on the floor of the mantle cavity carry medium-sized particles, which settle farther within the cavity, across to the right side where they are caught in forwardly directed currents and conveyed to the exhalent opening.

C. Frontal cilia on the gills and cilia on the folded surface of the hypobranchial gland carry the lightest particles, which still remain in suspension when the water passes between the gill filaments, across the roof of the mantle cavity. These minute particles become entangled in the mucus produced by the hypobranchial gland—hence the size and importance of this gland—and, so consolidated, are carried to the right side where they are conveyed forward and out together with the medium-sized particles and the faeces.

The relation of these three sets of currents to one another is shown diagrammatically in Fig. 1. It will be noted that the osphradium (o) represents the line of division between currents B and C.

The same general arrangement of rejection currents has been found in such typical pectinibranch Prosobranchia as *Littorina littorea*, *L. rudis*, *Nucella* (*Purpura*) *lapillus*, *Nassarius* (*Nassa*) *reticulatus* and *Buccinum undatum* by Mr G. C. E. B. Hulbert while working under the direction of the author. The only organ in the mantle cavity which shows marked variation in form is the osphradium. It is suggested, on biological grounds, that the function of the osphradium is to determine the amount of sediment which enters the mantle cavity (Hulbert & Yonge, 1937). This varies widely according to the habitat of the animal.

EVOLUTION OF CILIARY FEEDING

A consideration of the above facts has indicated the possible mode of origin of the ciliary feeding mechanisms which have been described in *Crepidula* and *Calyptraea* (Orton, 1912, 1914), *Vermetus novae-hollandiae* (Yonge, 1932), and briefly noted in *Capulus ungaricus* by Orton (1912). Further observations were made by the author on the last-named during a visit to the Bergens Museum Biological Station at Herdla in 1936, and also on specimens obtained from the marine laboratories at Plymouth and Millport. The author wishes to acknowledge his indebtedness to Prof. A. Brinkmann, Director of the Bergen Station, and also, for financial assistance, to the Colston Research Society, Bristol.

All of these animals are specialized herbivores. This fact is established by the universal presence in them of a crystalline style, characteristic (Yonge, 1932) of herbivorous Gastropoda "which feed by ciliary mechanisms, or by the slow but almost continuous action of a radula". Ciliary feeding representing a further specialization associated with a sedentary mode of life, it follows that we must consider the ancestors of animals feeding in this manner to have been primitive herbivorous prosobranchs, possessing styles, but probably feeding by means of a radula and jaws. The single pectinibranch gill of such a form would be concerned solely with its primitive function of respiration and ciliary currents in the mantle cavity only with rejection of sediment.

Such primitive herbivorous prosobranchs appear to have evolved in various directions. One line of evolution is represented by animals such as *Pterocera* and other Strombidae (Yonge, 1932): they possess a proboscis and use the jaws to crop fine algae which are broken down in the stomach by a cellulase. The radula shows little sign of wear "evidently acting as a conveyor belt" (Peile, 1937). Another line of evolution is represented by *Aporrhais* (Yonge, 1937), which burrows in mud and collects detritus of plant origin with the aid of an extensile proboscis possessing grasping jaws and radula. Other lines are represented by groups—not necessarily closely related to one another—which have lost the power of movement, either as a result of cementation to the substratum as in the Vermetidae, or effectively as in the Calyptraeidae and Capulidae. In these families, as in the Lamellibranchia, the gills and the ciliary currents in the mantle cavity have become modified to enable the animals to collect fine particles, chiefly phytoplankton, from the surrounding water.

Vermetus novae-hollandiae.

The simplest case would appear to be that of *Vermetus novae-hollandiae* (Yonge, 1932). This large species lives, cemented to dead coral rock, on the exposed outer faces of Indo-Pacific coral reefs. Unlike the smaller *V. gigas* which lives in still waters in the Mediterranean and, as recently conclusively demonstrated by Boettger (1930), collects plankton by means of long

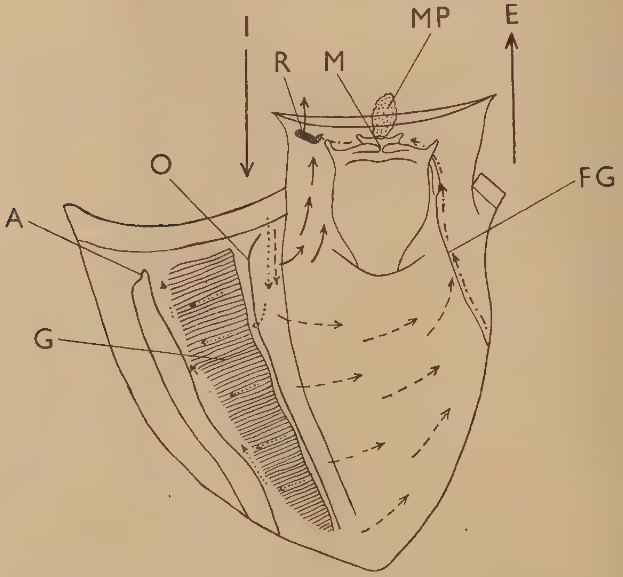


Fig. 2. *Vermetus novae-hollandiae*, mantle cavity opened along right side, seen from above. × 1½. A, anus; E, exhalent current; FG, food groove; G, gill; I, inhalent current; M, mouth; MP, mucus from pedal gland; O, osphradium; R, position where large particles collected prior to rejection by action of current A. Various currents represented by same type of arrows as in Fig. 1. (Figure modified after Yonge, 1932.)

mucous threads extruded from the pedal gland, *V. novae-hollandiae* is a ciliary feeder. As shown in Fig. 2, heavy material is accumulated on the left side of the head and then rejected; this represents current A. Medium-sized material is carried across the floor of the mantle cavity in current B, where it passes into a food groove which carries it to the mouth. Finely divided material—which will include phytoplankton on which the animal chiefly feeds—is carried by frontal cilia on the gill filaments to the free edge of the gill where other cilia carry it anteriorly. In life this free edge is in close apposition to the food grove (FG) on the right side of the mantle cavity. This current clearly represents a modification of current C. It should further be noted that there is *no* hypobranchial gland. The increased size of the gill—the result of its added function as a collector of food—leaves no space for this organ, which is in any case unnecessary because material is no longer passed completely across the roof of the mantle cavity but carried at right angles, anteriorly, along the free edge of the gill.

Food which enters the food groove from either current B or C is carried round the right-hand side of the head to the mouth (M). As food streams approach, the small introvert is extruded over the opening of the pedal gland, the mouth opens and the exposed radula seizes the food which has been mixed with mucus from the pedal gland (MP). Any excess of material passes farther to the left and joins the material rejected by current A. The secretion of the pedal gland, no longer required to provide lubrication for movement, is thus concerned with the consolidation of food particles but *not* with its direct capture as in *V. gigas*.

Crepidula fornicata and other Calyptraeidae.

In *Crepidula fornicata* (Orton, 1912, 1914) the elaboration of the ciliary feeding mechanisms has been carried several stages farther. The mantle cavity is of relatively enormous size, extending over the entire visceral mass and also over the elongated "neck" region. This provides for the accommodation of the gill, which is many times larger than that of typical prosobranchs of the same body size (it is also relatively larger than that of *V. novae-hollandiae*, though not to the same extent). This increase in the gill is due to the greater current needed for feeding and the increased surface for food collection. The modifications of the individual filaments will be discussed later. The osphradium (Fig. 3, O) is reduced to a small area at the anterior end of the gill, but an endostyle (EN) extends along the entire base of the gill.* This structure, described in detail by Orton (1912, 1914), is confined to the Calyptraeidae (*Crepidula* and *Calyptraea*) and represents a special adaptation for ciliary feeding in these animals, producing mucus which is carried on to the ventral, frontal surface of the gill filaments.

---

* In *V. novae-hollandiae* an elongated osphradium (Fig. 2, O) runs along the base of the gill, *not* an endostyle as described in my paper (Yonge, 1932). I am glad to have an opportunity of correcting this error. There are always abundant mucous glands in this region.

Food reaches the mouth by one of two routes. Large particles are carried direct into a food pouch (FP) in the mantle edge, which is situated, in life, just anterior to the mouth. They are there worked up into a pellet with mucus and passed to the mouth. If food is not required or excess of material is present, it is carried out by a current which runs parallel to and slightly anterior to the food pouch. It is clear that this feeding current represents a modification of rejection current A. Medium and fine particles are carried over the floor of the mantle cavity in current B, but chiefly, entangled in mucus secreted by the endostyle, by way of the frontal cilia of the gill filaments (i.e. current C). By both routes particles pass into the food groove (FG) and are carried forward by the combined action of its cilia and those on the tips of the gill filaments. The food particles are here worked up into pellets with mucus and are passed from time to time to the mouth (M). There they are grasped and passed into the buccal cavity by the radula and retained there by the jaws prior to swallowing. Peile (1937) has remarked on the absence of wear in the teeth of the radula in both *Crepidula fornicata* and *Calyptraea chinensis*. There is no trace of a hypobranchial gland.

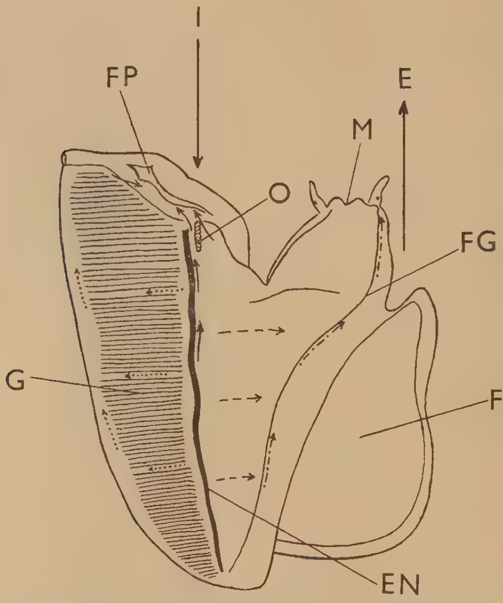


Fig. 3. *Crepidula fornicata*, mantle cavity opened along right side, seen from above. × 1½. EN, endostyle; F, foot; FP, food pouch. Other lettering as in Fig. 2. (Figure modified after Orton, 1914.)

Orton found essentially the same conditions in *Calyptraea* and they almost certainly prevail throughout the Calyptraeidae. Kleinsteuber (1913), in a comparison of the genera of this family, has pointed out that in *Calyptraea*, *Crepidula* and *Janacus* the length of the gill filaments is about one-half, in *Trochita* some three-quarters and in *Crucibulum* twelve-thirteenths the width of the body.

Capulus ungaricus.

The only existing account of feeding in this very interesting species being confined to a brief statement by Orton (1912), a more detailed account would appear to be well justified, apart from its importance in connexion with the general subject-matter of this paper. The animal has very limited powers of movement and is often found attached to the free edge of the valves of Lamellibranchia. The appearance of the animal from the dorsal aspect after the limpet-like shell has been removed is shown in Fig. 4, which also indicates the

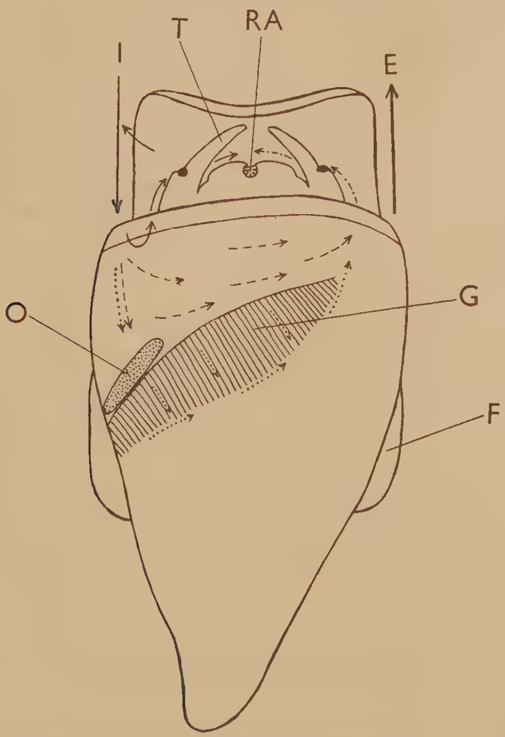


Fig. 4. *Capulus ungaricus*, animal seen from above after removal of shell; organs and currents in mantle cavity shown. ×3. RA, radula; T, tentacle. Other lettering as before.

position, within the mantle cavity, of the gills (G) and osphradium (O). The head with the stout tentacles (T) projects a little beyond the mantle edge. The position of the mouth and contained radula (RA) is shown but not that of the remarkable grooved proboscis. The proboscis appears in Fig. 5 (P), drawn after it and the foot had been extended anteriorly. It is formed of the prolonged lips and extends downwards, the tip lying on the flat, upper surface of the anterior prolongation of the foot. The gill is very large and extends obliquely across the roof of the mantle cavity, instead of along the left side as in a typical prosobranch or in the other ciliary feeding species. This would appear to be a direct consequence of its large size; it could not be accommodated in the restricted mantle cavity were it not so disposed. There is a conspicuous osphradium (Figs. 4 and 5, O) but no hypobranchial gland.

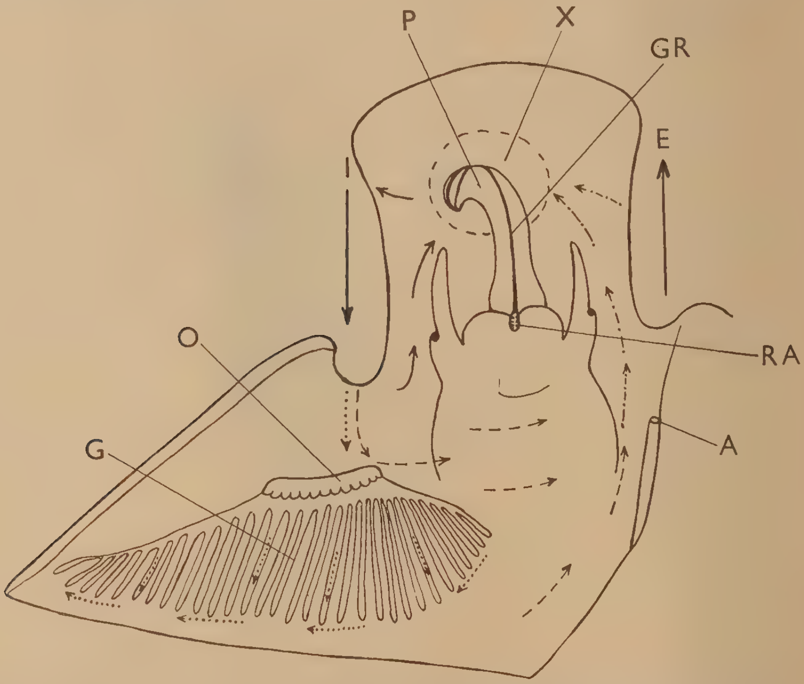


Fig. 5. *Capulus ungaricus*, mantle cavity opened along right side, seen from above. ×3. GR, groove along proboscis; P, proboscis; X, region of propodium, below proboscis, where food material collects. Other lettering as before.

The powerful inhalent current (I), created by the lateral cilia on the gill filaments, enters the mantle cavity on the left side and impinges almost at right angles on the obliquely situated osphradium. The heaviest suspended material does not reach this organ, but is caught in current A and carried round the upper surface of the anterior prolongation of the foot to the region of the tip of the proboscis. The osphradium represents the division between currents B and C, the former carrying medium-sized particles over the floor of the mantle cavity and the latter consisting of currents on the gills. These last currents are produced by frontal cilia which carry fine particles to the tips of the filaments; here particles come under the influence of currents caused by conspicuously large cilia and are conducted, embedded usually in mucous strings, along the tips of the filaments in an obliquely anterior direction towards the exhalent opening. There are also abfrontal cilia, smaller than those on the frontal surface, which carry particles to the tips of the filaments.

Material in currents B and C unites in a common stream near the exhalent opening and passes anteriorly round and beneath the head to join material from current A on the upper surface of the propodium (in the region marked X in Fig. 5). Material here collects in mucus-laden masses—sections reveal abundant mucous glands in and below the epidermis in this region—and on these the animal feeds by means of the proboscis. Food passes up the groove in the proboscis (GP) by means of ciliary, possibly aided by muscular, action; the radula appears to have an essentially conveying function. Peile (1937) states that in "*Capulus ungaricus* the teeth are slightly blunted in a few of the front rows".

Orton (1912) states that the proboscis "appears to be held along the right side of the animal to collect the food-particles from the tips of the gills when the animal is feeding". Nothing corresponding to this was observed in any of the three specimens examined. Orton, however, admits that he had no opportunity of investigating *Capulus* fully.

Unlike the Calyptraeidae further evolution within the Capulidae has been towards parasitism. Certain species of *Capulus* have been described as parasites, but this may be due to a misinterpretation of the true function of the proboscis; there is, however, no question as to the ecto-parasitic habits of all species of the allied genus *Thyca*. Here the animal is attached throughout adult life to the body of echinoderms. The foot is correspondingly reduced; the radula is lost, but the proboscis is elongated and penetrates deep into the body of the host, apparently sucking in the coelomic fluid (see Schepman & Nierstrasz, 1909; Koehler & Vaney, 1912). The species of the allied but completely sedentary family Hipponycidae probably feed in a similar manner to *Capulus*.

Modification of gill filaments.

The elaboration of ciliary feeding mechanisms in these Prosobranchia has involved, above all else, modifications of the gill filaments. The nature of these modifications can best be discussed by reference to Fig. 6, in which appear lateral views of complete filaments and also transverse sections near the base, from the gills of the three species already discussed. Similar figures of *Buccinum undatum*, as an example of a pectinibranch prosobranch in which the gills are exclusively concerned with their primitive function of respiration, are also given. The filaments of *Littorina littorea* and of *Aporrhais pespelecani*, which were also examined, do not differ essentially from those of *Buccinum*. Except for *Vermetus*, the drawings of the complete filaments were all made from living tissue.

The first point of interest is the progressive increase in the length of the filaments in comparison to width at the base. In *Buccinum* (Fig. 6 A), and similar Prosobranchia, the filaments are roughly triangular with the base and height about equal; the other extreme is represented by *Crepidula* (Fig. 6 D), where the filament is narrow throughout and greatly elongated. The ratio of height to maximum width is in *Buccinum* (A) 1:1, in *Vermetus* (B) 2·75:1, in *Capulus* (C) 3:1 and in *Crepidula* (D) 26:1. In *Vermetus* the figures given are based on measurements of preserved filaments which, as indicated by the transverse section, contract considerably in width; they are thus not strictly comparable with the others and the ratio should certainly be lower and so nearer to conditions in *Buccinum*.

In the general distribution of the main tracts of cilia, frontals (*f*), laterals (*l*) and abfrontals (*a*)—the last being always somewhat shorter and more sparse than the frontals—and in the presence of the internal chitinous supporting rods (*c*), the various filaments do not differ fundamentally. In all the frontals and abfrontals beat towards the tips of the filaments and the laterals transversely. In *Buccinum* the particles carried to the tip are then carried over farther to the right (when the gill is *in situ*) and so on to the hypobranchial gland as shown in Fig. 1. But in the other three genera particles are carried forward along the tips from filament to filament at the region marked *x* (indicated approximately only in *Vermetus*).

Passing to a more detailed examination of the individual filaments, in *Buccinum* (A) there are well-developed frontal, lateral and abfrontal cilia. Between the regions occupied by the last two is a wide area which is sparsely ciliated (as noted in living material but never revealed in sections). This region is chiefly notable for the presence of many large mucous glands (*m*) and the irregular nature of the epithelium, in sharp contrast to its regular arrangement in the other ciliated regions. Dakin (1912), who studied sections cut parallel to the longitudinal axis of the filaments, speaks of the epithelium of the gill leaflet (the frontal region), the area of ciliated cells (the lateral region) and the area of glandular cells. His sections did not pass through the abfrontal region. Within the cavity of the filament are many blood corpuscles and much coagulated blood plasma, notably in the "glandular" region, which is presumably concerned with respiration and also with the entangling, in mucus, of any particles which are carried between the filaments in the current created by the lateral cilia. There are no mucous glands in the frontal or abfrontal regions, although they are abundant at the sides of the abfrontal epithelium. Muscular activity was observed in living tissue and there

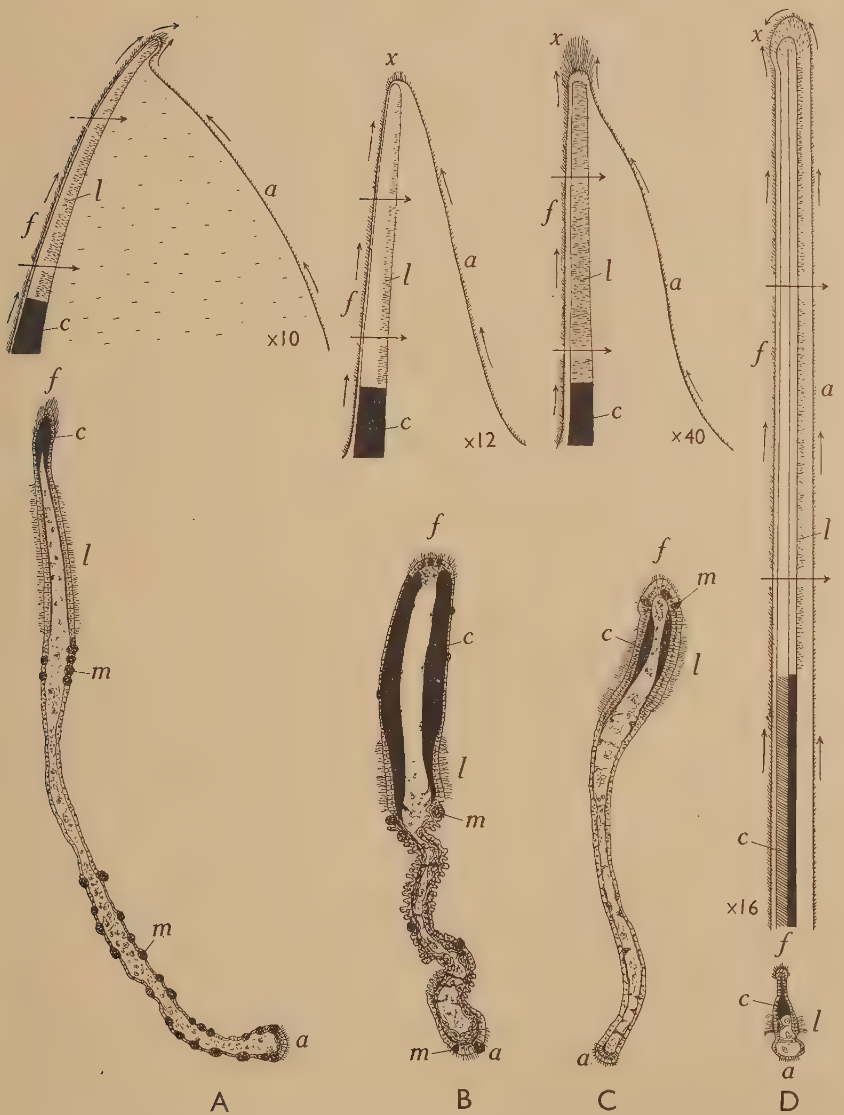

f
l
a
c
×10
x
f
l
a
c
×12
x
f
l
a
c
×40
x
f
a
l
c
×16
f
c
l
m
m
a
f
c
l
m
m
a
f
m
c
l
a
f
c
l
a
A
B
C
D

Fig. 6. Lateral view (above) and transverse section near base (below) of gill filaments of A, *Buccinum undatum*; B, *Vermetus novae-hollandiae*; C, *Capulus ungaricus*; D, *Crepidula fornicata*. Sections all ×55; magnifications of whole filaments shown in figure. *a*, abfrontal cilia; *c*, chitinous supporting rods; *f*, frontal cilia; *l*, lateral cilia; *m*, mucous gland cells; *x*, region of anteriorly directed current at tips of filaments.

are indications of muscle in the section, notably at the base of the abfrontal epithelium.

In *Vermetus* (B) the chitinous rods are exceptionally thick and broad and the area occupied by the lateral cilia is reduced and confined to the abfrontal third of the region supported by these rods. Mucous glands occur in all regions except in the epithelium which bears the lateral cilia. Their presence in both frontal and abfrontal epithelia indicates that their secretion assists in the entanglement of food particles in these regions. As already noted the filament has great powers of contraction, made possible by the presence, in the "glandular" and abfrontal regions, of longitudinal and transverse fibres and also others running across the central cavity. The wrinkled condition of the section indicates the effect of the contraction of the second and third of these sets of muscles.

In *Capulus* (C) conditions, in transverse section, approximate more to those in *Buccinum*, but mucous glands are here confined to the frontal region. It may be assumed, therefore, that collection of food particles by the frontal region is so efficient that few pass between the filaments, as they presumably do in the other two species. Muscle occurs, but not to the same extent as in the other two, although muscular movements were observed when living filaments were examined. An important feature is the great length of the terminal cilia, which exceed 100μ.

Finally in *Crepidula* (D), where the filament is no longer triangular, mucous glands are rare, a condition clearly correlated with the presence of the endostyle (Fig. 3, EN), a mucus-producing organ which has been described in detail by Orton (1912, 1914). The lateral cilia here lie nearer to the abfrontal region and beyond the region of the chitinous rods. There is little indication of muscle either in the behaviour of the living filaments or in sections. The tips of the filaments are flattened somewhat laterally, as shown in Fig. 6, but much more so dorso-ventrally, as described and figured by Orton (1912, Fig. 3). The filaments of *Crepidula* have clearly been modified to a much greater extent than those of *Vermetus* or *Capulus*.

The change in shape of the gill filaments from triangular to linear has had the important effect of increasing the extent of the region carrying lateral cilia—and so increasing the water current created in the mantle cavity—and also the extent of frontal and abfrontal regions, thereby augmenting the collecting surface. The accompanying reduction in the middle, or "glandular", region represents a reduction in the respiring surface. This is to some extent made good by the increased length of the gill (though not so in *Crepidula*) but, owing to the sedentary habits of these ciliary feeding Prosobranchia, the need for respiration will be distinctly less than that in actively moving genera, such as *Buccinum*. There is a tendency also for a relative increase in thickness of the chitinous supporting rods, necessary owing to the increased length of the filaments. The change in the distribution of the mucous glands may also be correlated in all three genera with feeding on fine particles, culminating in

Crepidula with the acquisition of an endostyle and the loss of mucous glands on the filaments. The change in the beat of the terminal cilia has already been noted.

It has thus been possible for the purely respiring gill filament of *Buccinum* and similar Prosobranchia to be converted into an organ of food collection by essentially minor modifications, representing the conversion of ciliated rejection tracts into food-collecting tracts. The process, incidentally, indicates the manner in which the gill of the Filibranchia and Eulamellibranchia probably evolved (starting from a paired aspidobranch gill and not from the unpaired pectinibranch gill here considered). The most important differences in these groups are the folding back of the filaments, their increased cohesion by means of interlamellar and interfilamentary junctions of various kinds, and the appearance of latero-frontal cilia. The latter, which appear to be universally present in these two groups, although very small in more primitive Filibranchia such as *Glycymeris* and *Arca* (Atkins, 1936), probably developed owing to the need for a straining mechanism, in the absence of which the narrow spaces leading to the suprabranchial cavity in these complex gills would become blocked. There is clearly no such need in the unfolded and unattached gill filaments of these Prosobranchia.

Discussion

The mode of feeding in the three families here discussed, the Vermetidae, Calyptraeidae and Capulidae, is in essentials the same, and undoubtedly represents a modification of ciliary mechanisms originally concerned with the rejection of sediment from the mantle cavity. There appears to be no reason for postulating a common origin for these families; the Vermetidae are admittedly widely removed from the other two, and they, though often grouped together (e.g. by Thiele (1925) in the Calyptraeacea), have many significant differences, their more superficial resemblances being very possibly the result of convergence due to similar modes of life and not of common origin. Lebour (1937) has recently shown that the larvae of *Capulus* possess an echinospira shell indicating relationship to the Lamellarioidea.

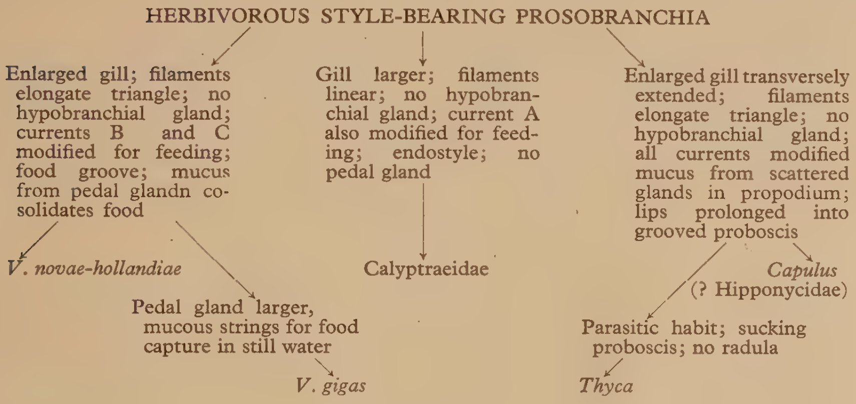
Modification of the ciliary mechanisms and associated changes are always correlated with complete or effective loss of the power of movement and with life in comparatively clear water. Loss of movement has involved the necessity of drawing food to the animal by means of ciliary currents (and by the unique method of mucous strings in *Vermetus gigas*), and this is possible only if the animal lives in water reasonably free from sediment which would clog the feeding tracts. Thus the Vermetidae live cemented to rocks and the Calyptraeidae and *Capulus* are frequently attached to the shells of Lamellibranchia, such as *Ostrea* or *Pecten*, or to stones, and so raised above the bottom deposits. Those living on Lamellibranchs will profit by the currents they create.

The necessity for providing powerful feeding currents and extensive collecting surfaces has been met by the elongation of the original broadly triangular gill filaments and by the greater extent of the entire gill. But there has been no change in the direction of the ciliary currents except for the anteriorly directed current along the tips of the filaments, a current which corresponds in function to those present in the food grooves along the free edges of the demibranchs in the Lamellibranchia. In the Calyptraeidae food collection has been further assisted by the appearance of an endostyle. In all genera current B, essentially unmodified, assists current C in the collection of food—a ciliated tract on the floor of the mantle cavity carrying food finally towards the mouth—while in all but the Vermetidae current A, by modification of its direction, also assists in this process.

The invariable absence of a hypobranchial gland, so very well developed in typical Prosobranchia, is correlated with the increased size of the gill, the filaments of which extend to the right side of the mantle cavity. Moreover, being an essential part of the original cleansing and rejection mechanism, as postulated in the case of *Aporrhais* (Yonge, 1937), it is no longer necessary.

The radula and jaws have been retained but are modified in function. Peile (1937) has described the conspicuous absence of wear in the teeth of the radula of all of these animals and concludes, "we may sum up the function of the radula as grasping, not rasping". Thus, although the gills have become modified in the direction of those of the Lamellibranchia and give some indication of the manner in which they have evolved, the actual taking in of food at the mouth consists of the grasping, by radula and jaws, of mucus-laden masses which are passed back into the oesophagus by the conveying action of the radula. Nothing in the nature of a selective mechanism, represented in the Lamellibranchia by the labial palps, the complex ciliated tracts on which rigorously control the passage of material to the mouth, has been evolved in these Gastropoda.

The evolution of ciliary feeding has taken significantly different directions in the three families. In the Vermetidae it is associated with a retention, and remarkable enlargement, of the pedal gland, which provides mucus for the consolidation of food particles in species such as *Vermetus novae-hollandiae*, while in *V. gigas* a still greater enlargement of this gland permits direct feeding by its secretion. In the Calyptraeidae the elaboration of ciliary feeding mechanisms has been taken to the highest degree of perfection recorded in the Prosobranchia: by the enlargement of the mantle cavity and of the gill, modification of the filaments, possession of an endostyle and conversion of all three rejection tracts into food streams. Finally in the Capulidae an increase in the size of the gill has been made possible by its oblique position in the mantle cavity; but the most characteristic feature is the remarkable grooved proboscis, the further evolution of which has resulted in the parasitic habit found in *Thyca*. The trends of evolutionary change in all three families may suitably be indicated diagrammatically as follows:



HERBIVOROUS STYLE-BEARING PROSOBRANCHIA

Enlarged gill; filaments elongate triangle; no hypobranchial gland; currents B and C modified for feeding; food groove; mucus from pedal glandn co-solidates food

V. novae-hollandiae

Pedal gland larger, mucous strings for food capture in still water

V. gigas

Gill larger; filaments linear; no hypobranchial gland; current A also modified for feeding; endostyle; no pedal gland

Calyptraeidae

Enlarged gill transversely extended; filaments elongate triangle; no hypobranchial gland; all currents modified mucus from scattered glands in propodium; lips prolonged into grooved proboscis

Capulus (? Hipponycidae)

Parasitic habit; sucking proboscis; no radula

Thyca

SUMMARY

1. Ciliary currents concerned with rejection of sediment from the mantle cavity of pectinibranch Prosobranchia consist of A, currents carrying heavier particles to the inhalent opening; B, currents carrying medium particles across the floor of the mantle cavity; C, currents carrying fine particles over and between the gill filaments for later consolidation by the mucus from the hypobranchial gland. Material in currents B and C is rejected from the exhalent opening.

2. The feeding currents in ciliary feeding Prosobranchia represent modifications of these rejection currents.

3. In *Vermetus novae-hollandiae* currents B and C only are modified, material being passed to the mouth region, where it is mixed with mucus from the large pedal gland, by way of a food groove.

4. In *Crepidula fornicata* and other Calyptraeidae all currents are modified for feeding and there is an endostyle for mucus secretion.

5. In *Capulus ungaricus* all currents are modified, food collecting on the upper surface of the propodium, where mucus is secreted and mucus-laden masses are passed to the mouth by way of the grooved proboscis.

6. In ciliary feeding species the gill is enlarged and the filaments tend to become longer and linear. This results in the production of an increased feeding current and collecting surface and the loss of the hypobranchial gland. Cilia at the tips of the filaments beat anteriorly. The distribution of mucous glands on the filaments can be correlated with the change in their function.

7. The possible mode of evolution of the lamellibranch gill is discussed in the light of these findings.

8. In the ciliary feeding Prosobranchia radula and jaws are retained for the grasping of the mucus-laden food masses; nothing equivalent to the labial palps of Lamellibranchia is present.

9. Evolution of ciliary feeding has probably been independently achieved in the three families considered. In the Vermetidae further development of the pedal gland enables direct mucus feeding, as in *Vermetus gigas*; in the Capulidae evolution culminates in a parasitic habit as in *Thyca*; only in the Calyptraeidae, where ciliary feeding mechanisms are most highly organized, do all genera and species appear exclusively to be ciliary feeders.

REFERENCES

Atkins, D., 1936. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part I. *Quart. Journ. Micr. Sci.*, Vol. lxxix, pp. 181–308.

Boettger, C. R., 1930. Studien zur Physiologie der Nahrungsaufnahme festgewachsener Schnecken. Die Ernährung der Wurmschnecke *Vermetus*. *Biol. Zbl.*, Bd. l, pp. 581–97.

Brockmeier, H., 1898. Süsswasserschnecken als Planktonfischer. *Plöner Forschungsber.*, Bd. vi, p. 165.

Dakin, W. J., 1912. *Buccinum. L.M.B.C. Mem.*, No. xx.

Hulbert, G. C. E. B. & Yonge, C. M., 1937. A possible function of the osphradium in the Gastropoda. *Nature*, Vol. cxxxix, p. 840.

Kleinsteuber, H., 1913. Die Anatomie von *Trochita*, *Calyptraea* und *Janacus*. *Zool. Jahrb.* Suppl. 13, *Fauna chilensis*, Bd. iv, pp. 385–476.

Koehler, R. & Vaney, C., 1912. Nouvelles formes de Gastéropodes ectoparasites. *Bull. Sci. France Belg.*, T. xlvi, pp. 191–217.

Lebour, M. V., 1937. The eggs and larvae of the British Prosobranchs with special reference to those living in the plankton. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 105–66.

Orton, J. H., 1912. The mode of feeding in *Crepidula*, with an account of the current-producing mechanism in the mantle cavity. *Journ. Mar. Biol. Assoc.*, Vol. ix, pp. 444–78.

—— 1914. On ciliary mechanisms in Brachiopods and some Polychaetes, with a comparison of the ciliary mechanisms on the gills of molluscs. *Journ. Mar. Biol. Assoc.*, Vol. x, pp. 283–311.

Peile, A. J., 1937. Some Radula problems. *Journ. Conch.*, Vol. xx, pp. 292–304.

Schepman, M. M. & Nierstrasz, H. F., 1909. Parasitische Prosobranchier der Siboga-Expedition. *Siboga-Expeditie*, Mon. XLIX^2.

Thiele, J., 1925. Prosobranchia. *Handbuch der Zoologie*, Kükenthal und Krumbach, Bd. v, pp. 40–94.

Yonge, C. M., 1926. Ciliary feeding mechanisms in the Thecosomatous Pteropoda. *Journ. Linn. Soc.* Lond., Zool., Vol. xxxvi, pp. 417–29.

—— 1932. Notes on feeding and digestion in *Pterocera* and *Vermetus*, with a discussion on the occurrence of the crystalline style in the Gastropoda. *Sci. Rpts. G. Barrier Reef Exped.*, Brit. Mus. (Nat. Hist.), Vol. i, pp. 259–81.

—— 1937. The biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.). *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 687–704.

Note. Since this paper went to press I have had the pleasure of seeing the manuscript of a forthcoming paper by Mr A. Graham on ciliary feeding in *Turritella communis*. Essentially the same mechanisms are involved as in the species here considered, but there are most interesting modifications due to the fact that this animal is adapted for ciliary feeding in a *muddy* environment.

THE FATE OF THE LARVAL ORGANS IN THE METAMORPHOSIS OF *OSTREA EDULIS*

By H. A. Cole, M.Sc.

Fisheries Experiment Station, Conway

(Text-figs. 1–8)

Introduction and Review of Previous Work

It has long been realized that the free-swimming larva of the European oyster (*Ostrea edulis*) must undergo considerable anatomical reorganization when it attaches itself as spat and takes on the fixed life of the adult oyster. The details of these changes have remained obscure. The fully developed "ansatzreifen" oyster larva has been admirably described and illustrated by Erdmann (1934). The smallest settled spat of which there is an adequate description is that figured by Yonge (1926). This specimen had a shell 1·2 mm. in length and must have been fixed for not less than 5 or 6 days, and possibly considerably longer; it had in most respects the structure of the adult oyster. It is clear that there is a considerable gap in our knowledge. A preliminary note by the writer (1937) gave information on a few points, particularly the rate of development of the gills and the changes in the adductor muscles. A further note (Cole, 1938) described a pair of sense organs of a new type found in the early fixed stages. In this, the first part of this study, the fate of the characteristic larval organs—the velum, foot, eyespots and adductor muscles—is described. The changes in gills, mantle, digestive system, etc., which take place during the first few days after attachment will be described in another publication.

Our knowledge of the metamorphosis of the larva of the American Atlantic oyster (*O. virginica*) is considerable, due chiefly to the efforts of Ryder (1882–84), Jackson (1888–90), and particularly Stafford (1913). In his monograph on *The Canadian Oyster* (*O. virginica*), Stafford gives a full account of the anatomy of both the fully developed larva and the earliest settled spat, and discusses the transition in detail. During recent years Prytherch (1934) has devoted further attention to this species. Although concerned mainly with the physiological requirements during attachment and metamorphosis, Prytherch gives a description and figure of the fully developed larva and discusses the fate of some of the larval organs, in particular the so-called pigment spots.

Roughley (1933) in his account of the life history of the Australian oyster (*O. commercialis*) gives a good description of the larva, but deals only briefly with the anatomical reorganization at fixation. The course of events in this species was in general so similar to that described by Stafford for *O. virginica* that he did not consider it necessary to give a detailed description. Hori (1926) gives some figures of the larva and spat of the common Japanese oyster (*O. gigas*) but does not consider the anatomical changes. In a later paper (1933) he describes also the development of the larva up to the setting stage in *O. lurida*, his figures being reproduced by Hopkins (1937). Although there are numerous other well-known species of oysters in no instance has the metamorphosis received any attention.

It has been customary (see Yonge, 1926) to assume that the metamorphosis of *O. edulis* follows very closely that of *O. virginica*, but it will be seen from the subsequent pages that this is not so, although it is possible that a re-investigation of certain points in the development of *O. virginica* may bring these two closely related species into line.

Material and Methods

The source of all material, both larvae and early spat, has been the oyster-breeding tanks of the Ministry of Agriculture and Fisheries at Conway. Since 1918 experiments in breeding *O. edulis* have been carried out in large concrete tanks, a description of which was published by the writer in 1936. Fully developed larvae were obtained by townet from the tanks and were fixed in Bouin's solution. No special precautions were taken to fix larvae in the expanded condition, since the collection of suitable material had to be carried out in odd moments during the summer when the breeding experiments were in progress. Larvae were simply dropped into tubes of Bouin's solution, and in practice the fixation was excellent and no trouble was experienced in determining the relations of the different organs in the contracted condition. For the study of the early spat stages, oyster shells which had been in the tanks a few days while settlement was in progress, and which were liberally sprinkled with spat, were immersed in Bouin's solution and later transferred to alcohol. In consequence of the decalcification of the surface layers of the shells, brought about by the acid in the fixative, it was later possible to brush off the spat without damage. Such shells yielded spat of all ages down to those which were in the act of settling, and, in fact, gave also some larvae which were merely wandering over the surface of the shell in search of a suitable place for attachment. More than a hundred such early spat were later embedded in paraffin and sectioned at a thickness of 8–10 μ. A large number of eyed larvae were also sectioned for comparison. No attempt was made to orientate the larvae or spat, as it was expected that a sufficient number would be cut in all planes to present an adequate picture of their anatomy. This in practice proved to be the case. Sections were stained with Ehrlich's acid haematoxylin and eosin. A large number of larvae and early spat were also prepared as whole mounts, Ehrlich's acid haematoxylin or alum-carmine being used for staining. A certain number of spat were caught on glass slides immersed in the tanks, and these slides were removed at known intervals and placed in fixative. These spat of known age were subsequently prepared as whole mounts and gave useful information on the speed of metamorphosis. Spat of known age for sectioning were obtained by immersing shells for fixed periods and later detaching the spat set thereon. Some aspects of the metamorphosis could be studied in living material, e.g. the disappearance of the eyespots, the growth of the shell and gills, etc.

The illustrations have in all cases been prepared from *camera lucida* drawings.

Brief Description of the Larva of *OSTREA EDULIS*

Although the fully developed oyster larva has been so well described by Erdmann, it will be necessary to give here a brief description of its outstanding features. The larva is characterized first of all by the possession of a large and muscular ciliated velum, which when protruded from the shell serves for both locomotion and food collection. When the shell is closed the velum occupies the fore-part of its cavity. The mouth is situated at the base of the velum on its *posterior* surface, between the velum and the foot—a long strap-shaped organ which develops only during the last day or so before attachment. The interior of the foot is occupied by the byssus gland which provides the secretion with which attachment is effected. On each side of the body of the larva a large eyespot develops a few days before attachment and is easily seen on account of the transparency of the shell and mantle at this stage. There are two adductor muscles, anterior and posterior, symmetrically placed in relation to the hinge. The anus is posterior, slightly dorsal to the posterior adductor. The nervous system in the larva consists of cerebral and pleural ganglia in the velum, pedal ganglia in the base of the foot, and visceral ganglia near the posterior adductor. There is a pair of statocysts in the base of the foot, near the pedal ganglia. Gills are not well developed in the larva, but Erdmann figures a row of six extremely short knob-like processes along the left side. During the process of attachment the larva comes to lie on the left or more convex valve of the shell.

The Velum

The fate of the velum of the lamellibranch larva, and in particular of its contained apical sensory area, has been the subject of considerable speculation. The suggestion that in *Ostrea* the velum was cast off was first put forward by Davaine (1852). A few years previously Lovén (1848) had suggested that in the forms studied by him the labial palps of the adult were derived from the apical area of the velum. This view was, however, rejected by later workers, among them Ryder (1882), who studied the metamorphosis of *O. virginica*, and it was not until the publication in 1901 of Meisenheimer's great work on the life history of *Dreissensia polymorpha* that the subject received the attention that it deserved. Meisenheimer described and illustrated the disintegration and absorption of the velum of *Dreissensia*, and showed clearly that the apical area was not lost but came to lie astride the oesophagus, and later fused with the upper lip of the mouth and did in fact form the basis of the labial palps.

Meisenheimer's work was apparently unknown in America for several years, as Sigerfoos (1908) and Stafford (1913), in discussing the metamorphosis of *Ostrea virginica,* make no reference to it. Sigerfoos, in his work on the development of shipworms (Teredinidae), refers incidentally to observations which he had made on *O. virginica.* He considered that the velum disappeared in its entirety very soon after attachment. He did not consider it possible that any part of the velum should give rise to the palps. Stafford (1913) gives a full account of the changes taking place at fixation in *O. virginica.* He states that after attachment the velum quickly atrophies, and in spat which had still in most respects the structure of the larva the velum was already shrunken and collapsed, the outline being rather vague. Immediately the spat began to grow, probably only a few hours after fixation, the velum was "so far gone as to be unrecognizable", and by the time the spat had increased its size by one-eighth "there remained only vestiges, chiefly of its muscles". Stafford discusses at length the possible loss of a part of the whole of the velum by "dehiscence", but came to the conclusion that no such "dehiscence" occurred. His material, however, was limited, consisting of sections of six spat only of the requisite size. Stafford, although unfamiliar with Meisenheimer's work, was acquainted with the views of Lovén regarding the origin of the palps. He was, however, of the opinion that the apical area of the velum played no part in the development of the palps. He found their origin in a thick-walled invagination dorsal to the oesophagus which later spread around and enveloped the mouth, giving rise to upper and lower palps by the growth of the outer and inner edges of the cavity. Concerning the interpretation of Stafford's sections further remarks will be made later in this paper.

Field (1922) in his study of *Mytilus edulis* came to the conclusion, from the examination of whole mounts only, that the labial palps of the adult were derived in the manner described by Meisenheimer. As far as I am aware no further attention has been paid to the subject during recent years.

A close study of my sections of very early spat makes it clear that in *Ostrea edulis* at least, the upper palps develop in a manner similar to that described by Meisenheimer for *Dreissensia.* Immediately after attachment the apical area of the velum becomes detached from the surrounding tissue and sinks into the interior of the velum, coming to lie dorsal to the oesophagus some distance from the surface of the body (Figs. 1 and 2). Here it is still associated with the cerebro-pleural ganglia of the larva. At the same time the velum collapses and is carried forward and upward by the rotation of the body. The mouth comes to lie just below the anterior adductor with the velar

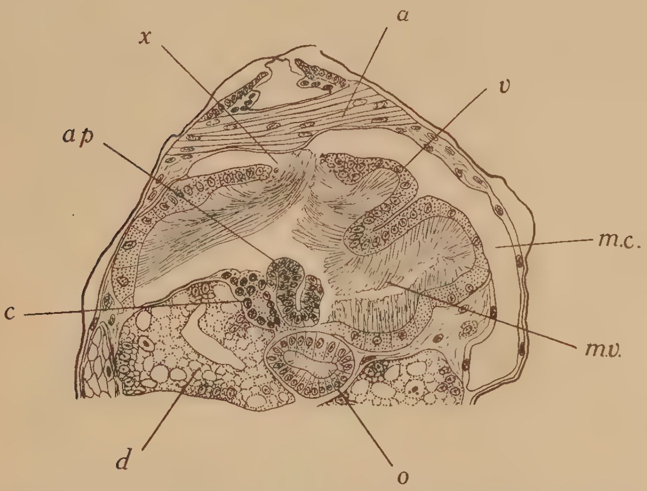


Fig. 1. Horizontal section of anterior end of oyster spat a few hours after attachment, showing the apical area of the velum detached from the surrounding tissues and lying astride the oesophagus. *a*, anterior adductor muscle; *ap*, apical area of velum; *c*, cerebro-pedal ganglion; *d*, digestive diverticulum; *m.c.*, mantle cavity; *m.v.*, muscle fibres of velum; *v*, velum; *x*, former position of apical area of velum.

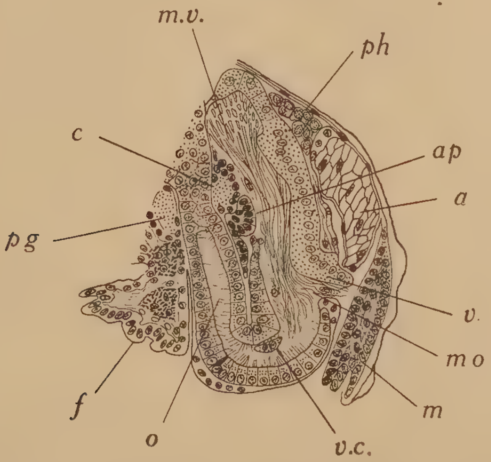


Fig. 2. Sagittal section of anterior end of oyster spat a few hours after attachment, showing the oesophagus bent round on itself, with the mouth directed inwards and blocked by velar muscles and detached cells. *a*, anterior adductor muscle; *ap*, apical area of velum; *c*, cerebro-pleural ganglion; *f*, foot; *m*, mantle; *mo*, mouth; *m.v.*, muscle fibres of velum; *o*, oesophagus; *ph*, phagocytes; *v*, velum; *v.c.*, detached velar cells.

remnants occupying a position between them. As the velar remnants sink more deeply into the body, the mouth, which is closely bound up with the stalk of the velum, is dragged in also and the oesophagus is for a while bent round so that the mouth faces inwards instead of outwards (Fig. 2). Due to the sinking of the apical area of the velum and the general collapse and disintegration of the latter organ, the muscle fibres which filled its cavity project from the body wall as a shaggy mass. While the mouth is bent inwards in the manner described above, it is practically blocked by these fibres and by detached velar cells, and, with the rapid dissolution of the velar tissues which is going on, it seems fairly certain that some of the remnants are swallowed. Such an occurrence would be by no means unusual in the metamorphosis of marine larvae. This bent position of the oesophagus does not persist for long, certainly not more than 24 hr., for the tension is relieved by the dis-

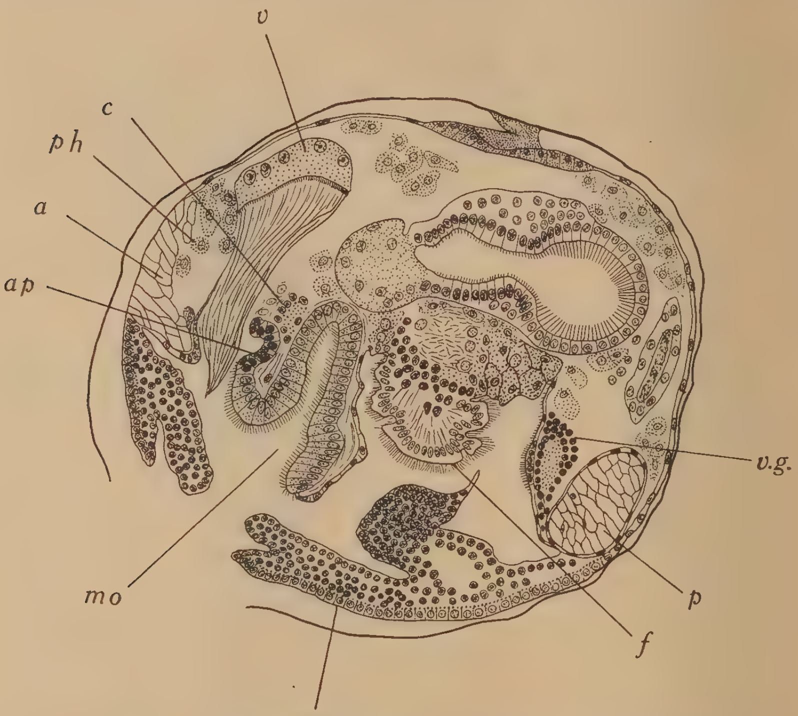


Fig. 3. Sagittal section of oyster spat about 24 hr. after attachment, showing the degenerating foot, the velar remnants practically enclosed within the body, and the apical area of the velum fusing with the upper lip of the mouth. *a*, anterior adductor muscle; *ap*, apical area of velum; *c*, cerebro-pleural ganglion; *f*, foot; *m*, mantle; *mo*, mouth; *p*, posterior adductor muscle; *ph*, phagocytes; *v*, velum; *v.g.*, visceral ganglion.

integration of the velar tissues. The apical plate moves along the oesophagus until it occupies a position directly above the mouth. Underlying it at this stage traces of the cerebro-pleural ganglia may still be seen. The apical plate now fuses with the epidermis of the upper lip (Fig. 3). At this stage, which is reached about 24 hr. after fixation, the velar remnants consist of a little of the typical epithelium of the thickened edge and some of the muscle fibres of the interior. These latter still project from the body wall between the mouth and the degenerating anterior adductor. Subsequently the much thickened upper lip spreads out laterally, and gives rise to short rounded lobes which project, one on each side, at the upper corners of the mouth (Fig. 5). These are the

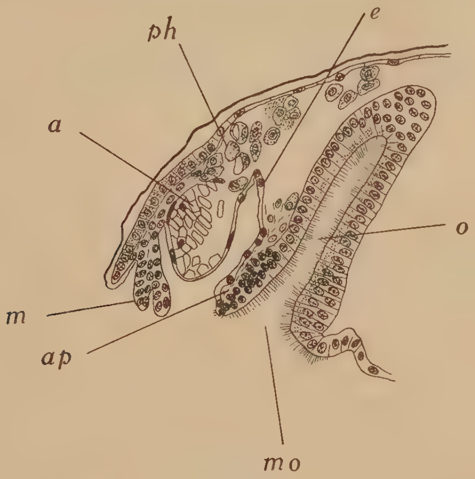


Fig. 4. Sagittal section of anterior end of oyster spat 48 hr. after attachment, showing the apical area of the velum completely incorporated with the upper lip of the mouth, and the epithelium of the body wall closed over the area formerly occupied by the velum. *a*, anterior adductor muscle; *ap*, apical area of velum; *e*, epithelium covering area formerly occupied by the velum; *m*, mantle; *mo*, mouth; *o*, oesophagus; *ph*, phagocytes.

rudiments of the upper, or outer, palps of the adult oyster. This stage is reached 48 hr. after attachment. During this period the velum also disappears completely, and a thin epithelium grows across between the palps and the remnant of the anterior adductor (Fig. 4). There can be no doubt that a great deal of the velar tissue breaks up and is lost or eaten. From a close study of Stafford's figures, and the text which accompanies them, I am of the opinion that it is not improbable that a re-examination of the development of the palps in *Ostrea virginica* will show that it follows a course very similar to that described above.

Later spat show the upper palps slightly more elongated and pointed (Fig. 6), the upper lip being drawn forward to form a hood over the mouth. Spat 3 or 4 days old show, however, no trace of the inner palps, unless the thickened

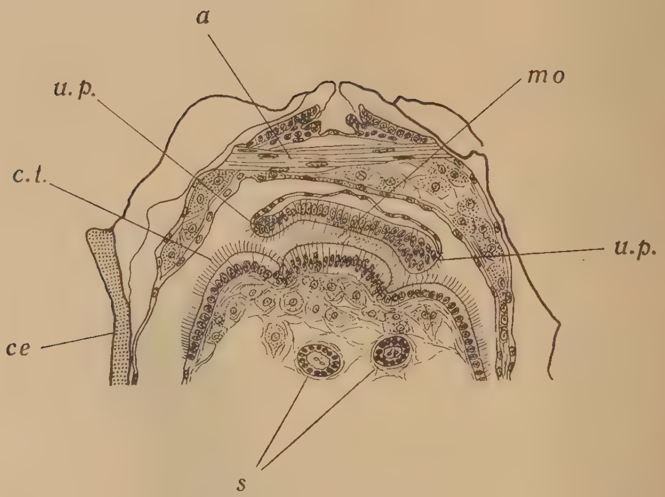


Fig. 5. Horizontal section of anterior end of oyster spat about 48 hr. after attachment passing just below the mouth, showing the lateral spreading of the upper palp rudiments, and the position of the statocysts. *a*, anterior adductor muscle; *ce*, cementing material; *c.t.*, ciliated tract at base of gills; *mo*, mouth; *s*, statocysts; *u.p.*, upper palps.

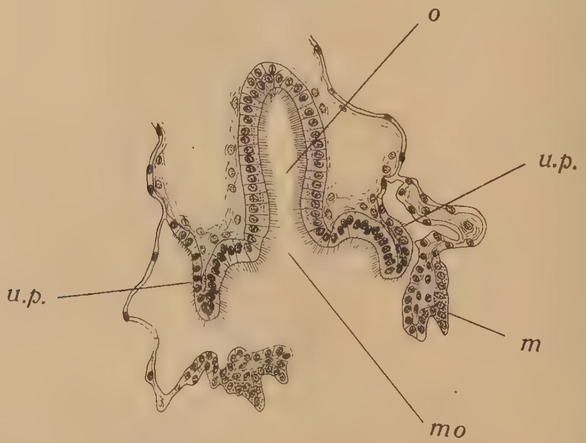


Fig. 6. Frontal section of oyster spat 3–4 days after attachment, showing the mouth and upper palps. *m*, mantle; *mo*, mouth; *o*, oesophagus; *u.p.*, upper palps.

nature of the rim round the mouth and in particular of the lower lip is an indication of their derivation from this source. In *Dreissensia* Meisenheimer states that the lower palps develop some time after metamorphosis as outgrowths from the upper palps. My material unfortunately does not extend beyond spat of 3–4 days old, none of which have the lower palps developed. These spat had shells about 0·6 mm. in length, while the smallest spat described by Yonge had a shell 1·2 mm. across. This individual had, however, relatively enormous palps, both upper and lower palps being well developed. It is probable that it had been settled not less than 5 or 6 days, but even so it is clear that the growth of the palps must be very rapid after the changes associated with metamorphosis have been completed.

The Foot

The foot develops very rapidly in the larva during the last 24 hr. or so before settlement. In the fully developed larva the foot is a long strap-shaped organ which projects from the body in the region between the mouth and the posterior adductor muscle. It is capable of being protruded between the valves for a distance at least equal to the diameter of the shell. Besides serving for locomotion on the substratum immediately prior to attachment, the foot is a highly sensory and glandular organ. The greater part of the base of the foot is occupied by the byssus gland which opens along the sole by a ciliated groove. Although the actual process of attachment in *Ostrea edulis* has not been described, there is no longer any doubt (see Erdmann, 1934) that this gland produces the cement with which the left shell of the larva is attached permanently to the substratum. Spat fixed to shells and subsequently detached by decalcification show a definite thick pad of homogeneous cement underlying the left valve (see Fig. 5). After fixation a little cement remains in the byssus gland and on staining takes up eosin with great avidity. The fate of this residual cement is easy to follow as in slightly more advanced spat phagocytes may be seen crammed with an eosinophilous substance which has every indication of being residual byssus material. The foot gradually shrinks in size following fixation and is carried forward by the rotation of the mouth until it occupies an almost mid-ventral position, projecting from the body wall behind the mouth as an irregular crumpled mass clothed with rather shaggy cilia (Fig. 3). The regular columnar epithelium which clothes the foot remains distinct for some time. Internally the pedal ganglia may be distinguished for about 24 hr. after fixation, although their outlines are rather vague. At this stage the glandular cells of the byssus cavity are also still quite distinct. In spat which have been attached 48 hr. the foot projects only slightly from the body and its free border is rather vague, suggesting the loss of some of the tissues making up the distal part. Internally, the tissues of the byssus cavity may still be seen, but the pedal ganglia are no longer distinguishable. The whole region is much invaded by phagocytes, some of which contain recognizable elements of the byssus gland. The last traces of the foot are absorbed and the epithelium assumes a smooth outline before the spat is 72 hr. old. The absorption of the foot in *O. virginica* is apparently not complete until much later, as Stafford states that traces may be seen in spat up to a size of 1 mm. Otherwise the details of the process appear to be very similar.

Of the sensory structures of the larval foot only the statocysts persist in the adult. In the larva they are closely applied to the sides of the pedal ganglia, although innervated from the visceral ganglia (Erdmann, 1934), and open on the base of the foot by a small pore. Following fixation and absorption of the foot they sink more deeply into the body until they come to lie below the root of the first gill filaments, ventral and slightly posterior to the mouth (Fig. 5). Their connexion with the exterior is lost. Such statocysts have already been described by Carazzi (1902) in the adult *O. edulis*, and were found also in *O. chilensis* by Dahmen (1923). I have received also a private communication from Prytherch which indicates their persistence in *O. virginica*. It seems probable that they are of frequent occurrence in oysters, although it is difficult to see what their function can be. They are stated not to occur in the adult *O. cucullata* (Awati & Rai, 1931). It is possible that they may serve as organs for the detection of movement in the surrounding medium, but the special pallial sense organs described by the writer (1938) would seem to be better equipped for this purpose, inasmuch as they are situated on the mantle and are separated from the external medium by a thin epidermis only, while the statocysts on the other hand are rather deeply set and must be correspondingly insensitive to small disturbances.

The Adductor Muscles

Huxley (1883) was the first to suggest that the single adductor of the early oyster larva did not correspond to the single adductor of the adult. The posterior adductor of the late larva was discovered by Jackson (1888) working with *O. virginica*. Since that time it has been recognized that the single adductor muscle of the early larva corresponds to the anterior adductor of dimyarian molluscs, while the adductor of the adult oyster corresponds to the posterior adductor of these forms. It has further been recognized that the late larva of all species of oysters possesses two adductors more or less symmetrically placed with regard to the hinge. In the eyed larva of *O. edulis* at the time of settlement the two adductor muscles are approximately equal in size. Following fixation the anterior adductor begins to degenerate and at the same time is crowded to the edge of the shell (Fig. 3). The posterior adductor enlarges and moves ventrally and anteriorly towards the centre of the shell. In spat which are between 24 and 48 hr. old the sizes of the posterior and anterior adductors are in the ratio of 3 : 2. Forty-eight hours after settlement a fringe (dissoconch) has usually been added to the larval shell or prodissoconch. Thereafter the degeneration of the anterior adductor proceeds rapidly. Spat which have been fixed 3 days usually show a few fibres only at the extreme edge of the shell, while at 4 days all traces of the anterior shell muscle have disappeared. The posterior adductor has increased in size and moved ventrally until it lies just outside the prodissoconch attached to the dissoconch or definite shell of the adult. Such 4 days' old spat may be 6 mm. in diameter. At this stage sections of the adductor muscle show no differentiation into "quick" and "catch" components.

The Eyes, with Remarks on their Function during Attachment

The eyes develop in the larva only during the last few days before settlement. They are a pair of spherical densely pigmented organs, situated in the body wall just dorsal to the attachment of the gill rudiments. In the living larva, when the velum is retracted, each eyespot can be seen underlying the valve of the shell at about its centre. The structure, function, and fate subsequent to metamorphosis of these organs have been the subject of considerable difference of opinion (see Prytherch, 1934). In *O. edulis* the eyes are described in detail and figured by Erdmann (1934), each eyespot consisting of an almost spherical cup of pigmented epithelium filled with a gelatinous matrix and having its aperture closed by a lens-like body. It gives the writer great pleasure to confirm Erdmann's description, as considerable doubt has been thrown upon his interpretation of their structure. The degree of pigmentation and the situation of the pigment in the epithelium of the cup appear to vary somewhat in different individual larvae. In some instances the nuclei of the epithelium are so densely pigmented as to show little structure, while the cytoplasm above the nuclei may be practically free from pigment. In others the pigment is dense in the cytoplasm while the nuclei are more lightly pigmented.

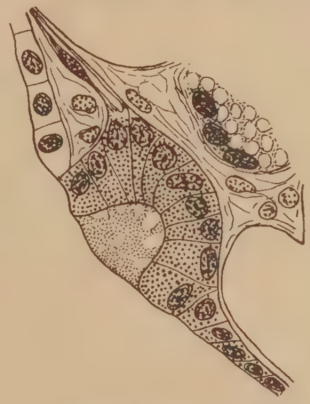


Fig. 7. Section through the eyespot of oyster spat just settled.

In a recent paper (1934) the structure of the eyespots in the larva of *O. virginica* is discussed in detail by Prytherch. He describes in this species pigment spots which are "found on each side of the body as very conspicuous larval organs". According to this author they have not the structure of eyes and have been incorrectly described as such. In support of his contention he states that in the course of experiments over a period of 8 years he has found no evidence that oyster larvae are sensitive to light intensity or colour. It must be admitted in this connexion that no such phototropic responses have been demonstrated in the larva of *O. edulis*, but this may largely be explained by the fact that the possibility of such responses existing has not yet been explored. There can, however, be no doubt whatever about the eye-like structure of the "pigment spots" in this species (see Fig. 7). Hopkins (1937) has studied experimentally the setting of larva of *O. lurida* under natural conditions, and concludes that "light is not an orienting factor in the setting behaviour of larvae of this species". Although he made no detailed study of the pigment spots he concludes that they are not light sensitive organs, and is inclined to support Prytherch's view that they have an entirely different function. Nelson (1925), on the other hand, is of the opinion that the eyed larva of *O. virginica* exhibits a negative phototaxis, which is not apparent in younger larvae without eyespots. Regarding the eyespot and its function Nelson states: "This spot, although unable to form an image like a true eye, is sensitive to light....In the presence of light these 'eyed' larvae of the oyster are stimulated and continue moving until they get into a shaded place, where they become quiescent." In this way he accounts for the preference exhibited by larvae for shady situations for attachment. It is clear, however, that the freedom of shady overhung situations from silt and encrusting growths is also an important factor in determining the density of settlement. Larvae of all species of oysters attach themselves only to clean surfaces, whether they are shaded or not. Roughley (1933) working with *O. commercialis* noted a tendency for the larvae to set in small depressions on the shells offered, as for example in the indentations between the teeth along the inner margins of the shells. A similar phenomenon has also been noted by Hopkins (1935). Roughley correlates this tendency with the increased protection against abrasion afforded by such situations. Hopkins (1935) has shown that the angle of inclination of the surface to the horizontal has an important effect on the intensity of setting in *O. lurida*. The more nearly the surface approaches the horizontal so does the intensity of setting on it increase. The present writer's experience with *O. edulis* in tanks has been similar, e.g. if two similar slates are put into the water, one at an angle of 45° and the other horizontal, then the intensity of setting on the under side of the horizontal slate will be considerably greater than on the same side of that set at an angle. Further, on the under side of the half-round limed tiles in use at Conway the intensity of setting is always greater along the ridge of the tile where the surface is horizontal, than along the sides where the surface is at an angle. The nature of the surface presented, i.e. whether it is rough or smooth, seems also to be of importance, and the writer has noticed that among some test slates placed horizontally in the Conway tanks, one which had been ground smooth caught far less spat than others the surfaces of which had not been touched. Hopkins (1935) further produces experimental evidence in support of his contention that the greater intensity of setting of *O. lurida* on the underside of horizontal surfaces is not due to negative phototaxis. He compared the setting on horizontal glass plates placed in the sea for 24 hr., some of which were coated on the upper surface with black paint, while others were plain. The results showed a slightly *greater* number of larvae setting on the underside of the plain glass in the unshaded situation. He considers that the greater intensity of setting on the underside of horizontal surfaces which is generally experienced to be due to the fact that larvae swim with the velum and foot uppermost and thus the foot most frequently comes into contact with horizontal surfaces. In a recent paper (1937) the same author gives further details of his experiments but the conclusions are the same. There is, however, a great deal of evidence for the view that larval oysters exercise some selection in the choice of the site to which they eventually become attached. They do not attach themselves to the first surface with which they come into contact as Hopkins implies. Before attachment larvae of *O. edulis*, and indeed apparently of most species of oysters, pass through an exploratory phase, during which they crawl over the surface of the substratum, with the foot protruded in front and apparently acting as an important tactile organ. Further, the writer is of the opinion that, in *O. edulis* at least, attachment may be postponed for a while if a suitable surface is not presented. Such an ability to delay metamorphosis until a suitable surface is available is possessed by the larvae of several species of polychaete worms, and in the opinion of Wilson (1937) has an important influence on the survival rate after metamorphosis. It is clear that the whole question of the factors influencing oyster larvae at the time of attachment needs to be examined more closely.

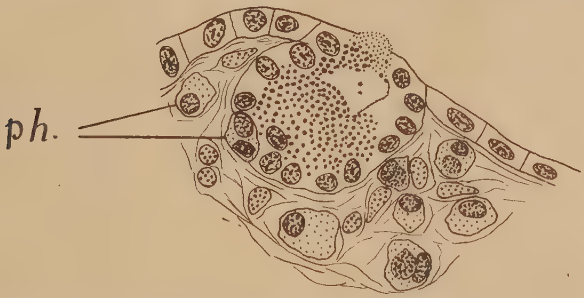


Fig. 8. Section through degenerating eyespot of oyster spat, a few hours after attachment. *ph*, phagocytes.

Prytherch describes in detail the dispersal of the pigmented cells in *O. virginica*, and their migration to the blood stream. In this species the break-up of the pigment spots is very rapid as the following statement shows: "When setting is in progress, the pigmented cells in each spot gradually enlarge, separate and one or two break away and are carried forward by the blood stream into the mantle. After attachment the pigment spot breaks apart more rapidly, and all the cells become distributed in a short time into the circulatory system, as the process of transformation of the larva is in full swing. Each pigment spot consists of approximately 300 cells, which after separation resemble in many respects the leucocytes of the spat and adult oyster." It is unfortunate that Prytherch should not have figured sections of larvae and early spat which would support his findings, but in a recent private communication to the writer he re-affirms his view that "these structures are not light sensitive organs, but function chiefly as leucocyte-generating tissue from which cells migrate to the blood stream during metamorphosis".

Concerning the fate of the eyespots Stafford offers no information, nor in fact does any writer other than Prytherch. In *O. edulis* the eyespots disappear as such after the first 24 hr. of attached life. Soon after attachment the eyes become less conspicuous due apparently to some loss of the black pigment. They tend also to sink below the epithelium of the body which later closes over them. There seems to be no reason to doubt that they are broken down *in situ* and the pigmented cells ingested by phagocytes. The details of this breakdown process naturally vary in different spat. The pigment usually disappears quickly from the nuclei. The outline of the epithelial cup becomes irregular and invading phagocytes may be seen (Fig. 8). With the breakdown of the cells, the pigment is liberated into the centre of the cup and lies in irregular clumps, the granules of which are considerably larger than those in the functional eye. Phagocytes are very numerous in the connective tissue underlying the eye. The final stages of the disintegration is represented by a group of phagocytes many of which contain cells and nuclei with much black pigment, which have every appearance of having formed part of the larval eyespot. That such phagocytes while still containing the remains of the pigmented epithelium of the eye may wander to other parts of the body is not unlikely, and this may create the illusion that the pigmented eye-cells are actually functioning as leucocytes. No separation and dispersal of the pigmented cells, such as Prytherch describes, has however been observed, the disintegration and absorption of the eyespots going on *in situ*.

SUMMARY

This is the first part of a study of the metamorphosis of the larva of the European flat oyster (*Ostrea edulis*) and deals with the fate of the larval velum, foot, adductor muscles and eyespots.

The apical area of the larval velum forms the basis of the upper labial palps of the spat.

The bulk of the velar tissue is broken up and cast off or eaten; the total dissolution of the velum being complete within 48 hr. of attachment.

The larval foot after effecting attachment rapidly shrinks in size and disappears within 72 hr. of attachment. Partial loss of its tissues probably occurs.

The statocysts persist in the spat.

Following fixation the anterior adductor muscle rapidly degenerates.

The so-called pigment spots of the larval oyster have the structure of eyes. During metamorphosis they degenerate rapidly *in situ*.

A discussion of the function of the eyespots during attachment reveals the need for further critical experiments.

REFERENCES

Awati, P. R. & Rai, S. H., 1931. *Ostrea cucullata* (The Bombay oyster). *Indian Zool. Memoir*, No. 3. Lucknow.

Carazzi, D., 1902. Contributo all' istologia e alla fisiologia dei lamellibranchi. *Intern. Monatschr. Anat. Phys.*, Bd. xx.

Cole, H. A., 1936. Experiments in the breeding of oysters (*Ostrea edulis*) in tanks, with special reference to the food of the larva and spat. *Min. Agric. Fish., Fish. Invest.*, Ser. II, Vol. xv, No. 4, pp. 1–25.

—— 1937. Metamorphosis of the larva of *Ostrea edulis*. *Nature*, Vol. 139, No. 3514, p. 413.

—— 1938. New pallial sense organs in early fixed stages of *Ostrea edulis*. *Nature*, Vol. 141, No. 3560, p. 161.

Dahmen, P., 1923. Anatomie von *Ostrea chilensis* (Phillipi). *Jena. Zeitschr. f. Naturwiss.*, Bd. lix, pp. 575–625.

Davaine, C., 1852. Recherches sur la génération des huîtres. *C.R. Soc. Biol.*, Paris, Vol. iv, p. 297.

Erdmann, W., 1934. Über die Entwicklung und die Anatomie der "ansatzreifen" Larve von *Ostrea edulis*, mit Bemerkungen über die Lebensgeschichte der Auster. *Wiss. Meeresunters. Abt. Helgoland*, N.F., Bd. xix, pp. 1–25.

Field, I. A., 1922. The biology and economic value of the sea mussel *Mytilus edulis*. *Bull. Bur. Fish.*, Washington, Vol. xxxviii, pp. 1–259.

Hopkins, A. E., 1935. Attachment of larvae of the Olympia oyster, *Ostrea lurida*, to plane surfaces. *Ecology*, Vol. xvi, pp. 82–7.

—— 1937. Experimental observations on spawning, larval development, and setting in the Olympia oyster, *Ostrea lurida*. *Bull. Bur. Fish.*, Washington, Vol. xlviii, pp. 439–503.

Hori, J., 1926. Notes on the full grown larva and the Japanese common oyster, *Ostrea gigas* Thunberg. *Journ. Imp. Fish. Inst.*, Vol. xxii, No. 1, pp. 1–7.

—— 1933. On the development of the Olympia oyster, *Ostrea lurida* Carpenter, transplanted from United States to Japan. *Bull. Jap. Soc. Sci. Fish.*, Vol. i, pp. 269–76.

Huxley, T. H., 1883. Oysters and oyster question. *Eng. Illust. Mag.*, Oct. and Nov., pp. 47–55, 112–21.

Jackson, R. T., 1888. Catching fixed forms etc. *Science*, Vol. xi, No. 275, p. 230.

—— 1889. The development of the oyster with remarks on allied genera. *Proc. Boston Soc. Nat. Hist.*, Vol. xxiii, pp. 531–56.

—— 1890. The phylogeny of the Pelecypoda. *Mem. Boston Soc. Nat. Hist.*, Vol. iv, pp. 277–400.

Lovén, S., 1848. *Archiv f. Naturg.*, Bd. xv.

Meisenheimer, J., 1901. Entwicklungsgeschichte von *Dreissensia polymorpha* Pall. *Zeitschr. f. wiss. Zoolog.*, Bd. lxix, pp. 1–137.

Nelson, T. C., 1925. *Rep. of the New Jersey Agric. Exp. Station*, pp. 281–8.

Prytherch, H. F., 1934. The role of copper in the setting, metamorphosis, and distribution of the American oyster, *Ostrea virginica*. *Ecol. Monogr.*, Vol. 4, pp. 47–107.

Roughley, T. C., 1933. The life history of the Australian oyster (*Ostrea commercialis*). *Proc. Linn. Soc. New South Wales*, Vol. lviii, pp. 279–333.

Ryder, J. A., 1882. Notes on the breeding, food and green colour of the oyster. *Bull. U. S. Fish. Comm.* 1881, Vol. i, pp. 403–19.

—— 1883. On the mode of fixation of the fry of the oyster. *Bull. U. S. Fish. Comm.*, Vol. iii, pp. 383–87.

RYDER, J. A., 1884. The metamorphosis and post-larval stages of development of the oyster. *Rep. U.S. Fish. Comm.* 1882, Vol. X, pp. 779–791.

SIGERFOOS, C. P., 1908. Natural history, organisation and late development of the Teredinidae, or shipworms. *Bull. Bur. Fish.*, Washington, Vol. XXVII, pp. 191–231.

STAFFORD, J., 1913. *The Canadian Oyster.* Ottawa.

WILSON, D. P., 1937. The influence of the substratum on the metamorphosis of *Notomastus* larvae. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 227–43.

YONGE, C. M., 1926. The structure and physiology of the organs of feeding and digestion in *Ostrea edulis*. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 295–386.

ON TWO SPECIES OF THE TREMATODE GENUS *DIDYMOZOON* FROM THE MACKEREL

By H. A. Baylis, M.A., D.Sc.

Department of Zoology, British Museum (Natural History)

(Text-figs. 1–6)

Taschenberg (1879) briefly described, under the name of *Didymozoon scombri*, a trematode which he recorded as occurring in pairs in cysts on the inside of the gill-covers of *Scomber colias* at Naples. Odhner (1907) found what he believed to be the same species not uncommonly in small specimens of *S. scombrus* off the west coast of Sweden, but was unable to find it in the larger fish taken in the early summer. He gives a minute description and excellent figures of the worm. Johnstone (1914) has also given a good, though diagrammatic, figure of its anatomy. Odhner describes the worm as occurring most commonly in paired cysts on the upper pharyngeal bones, but also in exceptional cases in cysts on the inside of the gill-covers and on the outside of the head, close behind the eye. About half the cysts examined by him contained two worms, the rest from three to seven. Johnstone describes the cysts as being most commonly situated "on the roof of the mouth beneath the pharyngo-branchials", but also sometimes on the basi-branchials, on the external surfaces of other parts of the gill-bars, or on the internal surface of the operculum. One cyst contained as many as sixteen worms. According to Dollfus (1926), he and Monod found cysts containing one, two, three or more worms in the mucosa of the mouth, palate and gills of *S. scombrus*, and also single unencysted worms under the transparent skin behind the eye.

Thus at least two authors record the same worm as occurring both inside the mouth and on the outside of the head, behind the eye. The writer has observed specimens in both situations in mackerel (*S. scombrus*) from the English Channel, but considers that they represent two different species. By far the commonest occurrence is to find a pair of cysts in the roof of the pharynx, at the anterior end of the pad which carries the upper pharyngeal teeth. The symmetrical position of these cysts suggests that they occupy a pair of organs normally present in the mackerel—in all probability a pair of lymphatic glands. A variable number of worms may be found in each cyst, and these vary considerably in size. They agree in all essential features with the descriptions given by Odhner and by Johnstone, and are considered to belong to the species *scombri* Taschenberg, 1879, *sensu* Odhner.

In a small percentage of the mackerel examined one or more elliptical yellowish bodies, about 3–7 mm. long and 1–1·5 mm. wide, were observed beneath the transparent outer skin of the head, behind the eye. These, on being dissected out, were found to be cysts containing from one to four worms closely resembling *Didymozoon scombri*, but differing from it in a number of respects. The worms are very tightly packed in the cyst. Moreover, the cyst-wall is relatively tough and the worms extremely fragile, so that in preserved material it is almost impossible to extract the worms without damaging them. Further, the same cyst often contains two or more worms so enormously different in size that it is very difficult to detect the small individuals and to separate them from the large, to which, when preserved, they may be firmly adherent. These difficulties, however, can be overcome by opening the cysts in the fresh condition, when the worms are usually quite readily separated.

The following is a description of the species occurring in these "facial" cysts, which it is proposed to name

Didymozoon faciale, sp.n.

The length of the worms (after mounting in Canada balsam) varies between about 0·71 and 16·3 mm. The largest individuals measure (when slightly flattened under cover-glass pressure) up to about 1·4 mm. in maximum width, the smallest only 0·08 mm. Specimens under 3 mm. in length are generally without eggs, and in most of them the female portions of the genital apparatus are undifferentiated. The testes, however, are generally well developed and functional. This was so even in a specimen only 1·1 mm. long (Fig. 2). While in one specimen 4·6 mm. long even the testes could not be made out, another measuring only 3 mm. in length already had fully-developed female organs and was producing eggs. In the smallest specimen seen, which was 0·71 mm. long, the testes appeared to be quite undifferentiated. Fig. 1 gives an idea of the variation in size which may occur among the worms in a single cyst. In some the disparity is even greater, a minute "male" worm little more than a millimetre long being found together with a fully-developed hermaphrodite individual measuring up to about 16 mm.

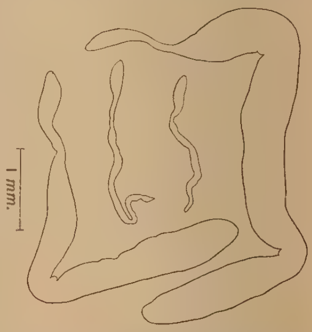


Fig. 1. *Didymozoon faciale*. Outlines of the four individuals from a single cyst, drawn to the same scale, to show relative sizes.

The anterior portion, or "forebody", is somewhat flattened dorso-ventrally and lanceolate in outline. It is joined by a narrower "neck" to the "hindbody", which is generally cylindrical. With increasing age the "hindbody" undergoes much more rapid growth than the "forebody", so that in a large worm there is a much greater difference in their relative proportions than in small specimens. The larger individuals, owing to their close confinement within the cyst, are generally bent sharply upon themselves in two places, so that the anterior and posterior ends tend to overlap.

At the anterior extremity there is a small oral sucker (Figs. 2, 3, 4, 5, *su*). This is oval or pear-shaped, instead of being subglobular, as in *D. scombri*. It is also very much smaller than in that species. It measures 0·04–0·08 mm. in length and 0·03–0·052 mm. in maximum width, its dimensions being roughly proportional to the size of the specimen.* The sucker is immediately followed by a small hemispherical pharynx (Fig. 5, *ph*), measuring about 0·018–0·024 mm. in diameter.† A narrow oesophagus connects the pharynx with the intestine, which at its anterior ends forms a wide tube running transversely (Figs. 2, 4). From this two caeca (*c*) run posteriorly as delicate, thin-walled tubes which are thrown into numerous short dorsoventral loops, giving them a sacculated or moniliform appearance. The caeca are conspicuous only in the forebody, and, except in the youngest and smallest specimens, are difficult to detect in the hindbody, almost the whole of which is occupied by the genital apparatus. The excretory system has not been made out.

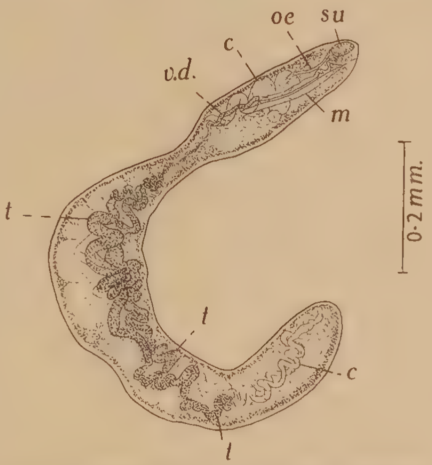


Fig. 2. *Didymozoon faciale*. Young specimen in which only the male organs are fully developed. *c*, intestinal caecum; *m*, metraterm; *oe*, oesophagus; *su*, sucker; *t*, testes; *v.d.*, vas deferens.

The arrangement of the genital organs is the same as in *D. scombri*. Ventrally to the oral sucker there is, in the medium-sized and larger specimens, a rounded muscular papilla (Figs. 3 and 4, *p*) on which the genital pore is situated. Running almost straight back from this papilla down the middle line of the forebody is the metraterm (Figs. 2, 3, 4, *m*), or terminal portion of the uterus. This is apparently the first part of the female genital apparatus to be differentiated, and is visible even in such a young specimen as that shown in Fig. 2. It has, for the greater part of its length, a rather stout coat of circular muscles, but the muscles become sparser near the anterior end. Dorsally to the metraterm, and running roughly parallel to it, but with a more convoluted course, is the vas deferens (Figs. 2, 3, 4, *v.d.*). This also has a somewhat muscular wall, but is a much narrower and more transparent tube than the metraterm. Passing through the narrow "neck" of the worm, it divides just behind it into two vasa efferentia, each of which is continuous with one of the two long, coiled, tubular testes (Figs. 2, 3, *t*). In young specimens (Fig. 2) these occupy the greater part of the body. In older individuals (Fig. 3), however, owing to the great growth of the hindbody, they extend only about as far as the anterior third of the total length.

---

* In *D. scombri* Odhner (1907) found the diameter of the sucker to be 0·3–0·4 mm. From the scale of magnification it appears to have been about 0·47 mm. long and 0·53 mm. wide in the specimen figured by Johnstone (1914). In specimens examined by the writer it measures 0·21–0·6 mm. in length and 0·25–0·55 mm. in width. Johnstone gives the dimensions of the worms as 15–20 × 0·5–over 1 mm., Odhner as 25–35 × 1·2–1·75 mm. The writer has seen much larger specimens, one of which measured 55 mm. in length and 2 mm. in breadth when mounted in balsam.

† In the writer's specimens of *D. scombri* the pharynx has a diameter of 0·08–0·1 mm. It is difficult to detect in the larger specimens when mounted whole, as it appears to become hidden by a dense coat of cells, and also to become more intimately fused with the sucker. According to Odhner its diameter is 0·06 mm.; according to Johnstone's figure apparently about 0·14 mm.

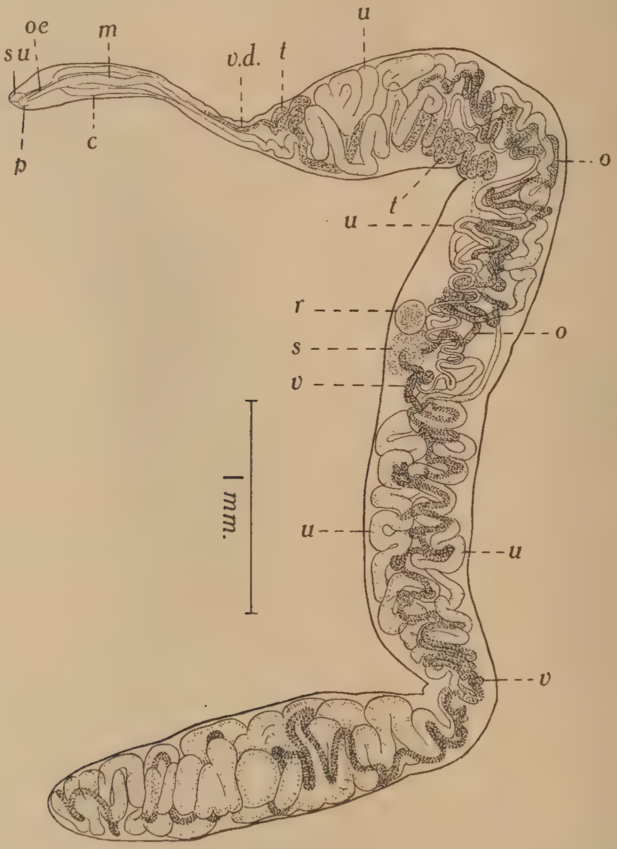


Fig. 3 *Didymozoon faciale*. Mature hermaphrodite individual. *c*, intestinal caecum; *m*, metraterm; *o*, ovary; *oe*, oesophagus; *p*, genital papilla; *r*, receptaculum seminis; *s*, shell-gland; *su*, sucker; *t*, testis; *u*, uterus; *v*, vitelline gland; *v.d.*, vas deferens.

The ovary (Fig. 3, *o*) and the vitelline gland (*v*) are both long, convoluted, tubular organs, the former beginning some distance in front of the posterior ends of the testes, the latter close to the hinder extremity of the body. They converge towards a point a little in front of the middle of the body, where they are connected with the oviduct, with which are also connected the "shell"-gland (*s*) and a well-developed and more or less globular receptaculum seminis (*r*). The uterus runs forward from the shell-gland complex as a much convoluted tube almost to the anterior end of the hindbody. Here it doubles back and runs to the extreme posterior end, whence it doubles forward and pursues a much convoluted course to about the level of the shell-gland complex. From this point it appears to straighten out somewhat, and its terminal portion forms the metraterm, as already described.

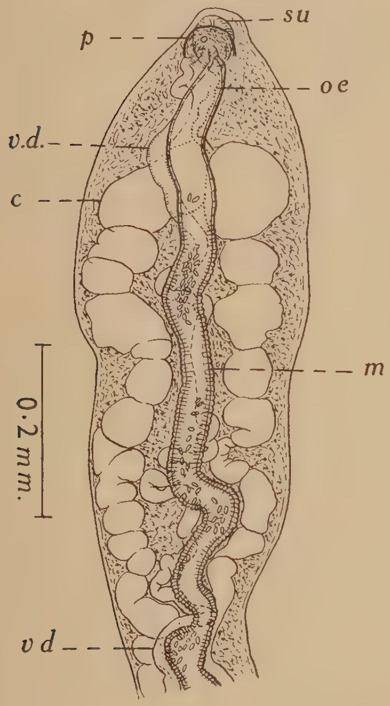


Fig. 4.

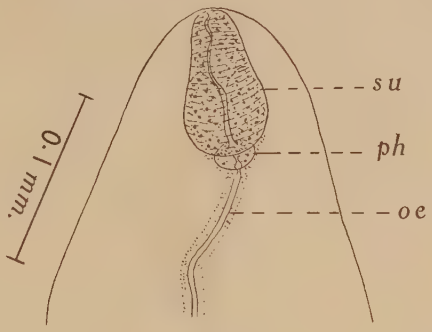


Fig. 5.

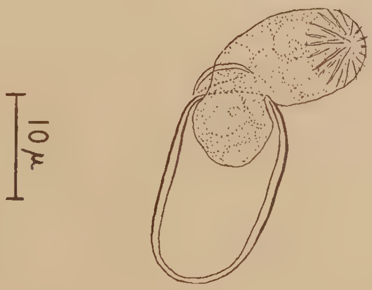


Fig. 6.

Fig. 4. *Didymozoon faciale.* Forebody of mature specimen; ventral view. *c*, intestinal caecum; *m*, metraterm *oe*, oesophagus (dotted outline); *p*, genital papilla; *su*, sucker; *v.d.*, vas deferens.

Fig. 5. *Didymozoon faciale.* Anterior extremity, showing *su*, sucker; *ph*, pharynx, and *oe*, oesophagus.

Fig. 6. *Didymozoon faciale.* Egg, with embryo escaping under pressure of cover-glass.

The eggs are exceedingly numerous and very small. Their shells are relatively thick and of a yellow colour, and are almost elliptical in shape. They measure about 0·018–0·02 × 0·011 mm.,[*] and have an operculum at one pole. In embryos liberated from the shells by cover-glass pressure (Fig. 6), it appeared possible to confirm an observation made by Wagener (in Lieberkühn, 1854) regarding a related species found in the flying-fish, *Exocoetus exsiliens*. Wagener describes and figures a crown of fine spines or hooks, "wie ein Tänienhakenkranz", round the "head" of the embryo. Under high magnifications the appearance of such a crown of spines was seen in the embryos both of *Didymozoon faciale* and of *D. scombri*. Owing to their minute size it was not possible to determine the precise form of these spines, or their number, but they appeared to be of two sizes, the longer and shorter spines alternating.

TAXONOMY AND NOMENCLATURE

After a study of the literature the generic name *Didymozoon* Taschenberg, 1879, has been provisionally adopted for the species described above. Odhner (1907) designated the species *scombri* as type of *Didymozoon*, and the genus has been accepted in this sense by Dollfus (1926) and other authors. Ishii (1935), on the other hand, refers *scombri* to *Nematobothrium* v. Beneden, 1858,[†] at the same time retaining *Didymozoon* Taschenberg (which he unnecessarily emends to *Didymozoum*) as an independent genus, with *D. sphyraenae* Taschenberg as its genotype.[‡]

According to Stiles & Hassall (1908), Taschenberg, in erecting the genus *Didymozoon*, was merely renaming the genus *Wedlia* Cobbold, 1860, and the type of both these genera is *Wedlia bipartita* (Wedl, 1855). This species is the first mentioned under the genus *Didymozoon* by Taschenberg, who renames it *D. thynni*. Moreover, he quotes Cobbold's reference and mentions that that author had referred this species to *Wedlia*. Poche (1926), however, rejects the suggestion of Stiles & Hassall, and points out that Taschenberg neither expressly states that he is renaming *Wedlia* nor admits that *Wedlia* and *Didymozoon* are synonymous. It is true that Taschenberg does not definitely designate a genotype of *Didymozoon*, and unfortunately Cobbold (1860) also fails to make a definite designation in the case of *Wedlia*, though from his text it is quite evident that he regarded *bipartita* as the typical species.

---

[*] The eggs of *D. scombri* are slightly smaller, measuring 0·016–0·0175 × 0·01–0·0105 mm., or, according to Odhner, 0·015 × 0·01 mm.

[†] Within the genus *Nematobothrium* Ishii proposes two new subgenera, *Benedenozoum* and *Maclarenozoum*, placing *scombri* in the former. Article 9 of the International Rules of Zoological Nomenclature lays down that "if a genus is divided into subgenera, the name of the typical subgenus must be the same as the name of the genus". Hence the subgenus *Benedenozoum*, which contains the genotype of *Nematobothrium*, is incorrectly named, and should be called *Nematobothrium*.

[‡] Yamaguti (1934) also defines *Nematobothrium* and *Didymozoon* as distinct genera, and gives *D. auxis* Taschenberg as "type by elimination" of the latter.

Didymozoon cannot, therefore, be disposed of without question as a synonym of *Wedlia*.*

The question whether *Didymozoon* (*sensu* Odhner) and *Nematobothrium* are congeneric cannot, as it seems to the writer, be determined without a fuller knowledge of the morphology of *N. filarina* v. Beneden, the type of *Nematobothrium*. v. Beneden's (1858, 1861) description of this form is admittedly very incomplete, and the species does not appear to have been redescribed. v. Beneden was unable to find even an oral sucker or an intestine, whereas some of the species attributed to *Nematobothrium* by later authors possess not only these organs but also a ventral sucker.

Although Ishii (1935) places *Nematobothrium* and "*Didymozoum*" in distinct subfamilies, his diagnoses of these two genera are almost identical, and the distinctions between them and between the subfamilies appear to be based on extremely unsatisfactory characters. The diagnosis of *Nematobothrium*, however, is necessarily based mainly on species other than the genotype, while "*Didymozoum*", as we have seen, is quite different from the *Didymozoon* of Odhner.

Yamaguti's (1934) definition of *Didymozoon* appears to be based mainly on the characters of a new species (*D. minor*) described by him, and in any case his designation of *D. auxis* Taschenberg as genotype is inadmissible in view of Odhner's earlier designation of *D. scombri* (*vide* International Rules of Zoological Nomenclature, Art. 30, II, *g*). The same remark applies to Ishii's designation of *D. sphyraenae*.

In view of these considerations it seems best to retain *Didymozoon*, *sensu* Odhner, as distinct from *Nematobothrium* v. Beneden, until more conclusive evidence is brought forward to show that these genera are identical. The new species here described is unquestionably congeneric with the *Didymozoon scombri* of Odhner, and is therefore referred to *Didymozoon*.

For the material on which this paper is based the writer is greatly indebted to Mr P. G. Corbin, of the Laboratory of the Marine Biological Association, Plymouth, and to Miss Miriam Rothschild. For some excellent preparations of *Didymozoon scombri* thanks are due to Mr L. A. Harvey, of University College, Exeter; and for a remarkably good preparation of *D. faciale* the writer wishes to thank Mr W. J. Rees, of the Plymouth Laboratory. The specimens of both species collected by Mr Corbin and by Miss Rothschild came from mackerel landed at Plymouth and at Newlyn in November 1936 and in February, March, May, October and November 1937.

---

* *Wedlia* is reduced by Ishii (1935) to a subgenus of *Köllikeria* Cobbold, 1860, the only other subgenus being named *Köllikerizoum*. This action again contravenes Article 9 of the International Rules, since there is no subgenus *Köllikeria*. The genotype of *Köllikeria* (*K. filicollis*) is placed in *Köllikerizoum*, which name consequently must be replaced by *Köllikeria*. On similar grounds Ishii's subgenus *Atalosparganum* should be replaced by *Atalostrophion* MacCallum, 1915.

REFERENCES

BENEDEN, P. J. VAN, 1858. *Mémoire sur les Vers intestinaux.* Paris, viii+376 pp., 28 Pls. Also in *Compt. rend. Acad. Sci.*, Paris, Suppl., II (1861), pp. 1–376, Pls. I–XXVII.

COBBOLD, T. S., 1860. Synopsis of the Distomidae. *Journ. Proc. Linn. Soc. London*, Zool., v, pp. 1–56.

DOLLFUS, R. P., 1926. Sur l'État actuel de la Classification des Didymozoonidae Monticelli, 1888 (=Didymozoidae Franz Poche, 1907). *Ann. Parasitol.*, Paris, IV, pp. 148–61.

ISHII, N., 1935. Studies on the Family Didymozooidae (Monticelli, 1888). *Jap. Journ. Zool.*, VI, pp. 279–335.

JOHNSTONE, J., 1914. Internal Parasites and Diseased Conditions of Fishes. *Proc. & Trans. Liverpool Biol. Soc.*, XXVIII, pp. 127–44, Pls. I–V.

LIEBERKÜHN, N., 1854. Ueber die Psorospermien. *Arch. f. Anat., Physiol. u. wiss. Med.*, Berlin, pp. 1–24, Pls. I, II.

ODHNER, T., 1907. Zur Anatomie der Didymozoen: ein getrennt-geschlechtlicher Trematode mit rudimentärem Hermaphroditismus. *Zoologische Studien Prof. T. Tullberg gewidmet*, Uppsala, pp. 309–42, 1 Pl.

POCHE, F., 1926. Das System der Platodaria. *Arch. f. Naturg.*, Abt. A, XCI, pp. 1–459, Pls. I–VII.

STILES, C. W. & HASSALL, A., 1908. Index-catalogue of Medical and Veterinary Zoology. Subjects: Trematoda and Trematode Diseases. *U. S. Hyg. Lab. Bull.*, No. 37, 401 pp.

TASCHENBERG, E. O., 1879. *Didymozoon*, eine neue Gattung in Cysten lebender Trematoden. *Zeitschr. f. Gesammt. Naturwiss.*, Berlin, LII ((3) IV), pp. 605–17, Pl. VI.

YAMAGUTI, S., 1934. Studies on the Helminth Fauna of Japan. Part 2. Trematodes of Fishes, I. *Jap. Journ. Zool.*, V, pp. 249–541.

ON THE SEASONAL ABUNDANCE OF YOUNG FISH. V. THE YEAR 1937

By F. S. Russell, B.A., F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–4)

The present report continues the observations on the seasonal abundance of the pelagic young of teleostean fish in the plankton off Plymouth (Russell, 1937) and gives the results for the year 1937. These results are published in the same form as in previous reports. The dates on which collections were made with the 2-metre stramin ringtrawl are given in Table I and the monthly average catches of the young fish per half-hour haul in Table II. In Fig. 1 is given the curve for the average catches for each fortnight of all young fish, excluding clupeids, and superimposed upon this the corresponding curve for the average catches over the period 1930–1934 inclusive.

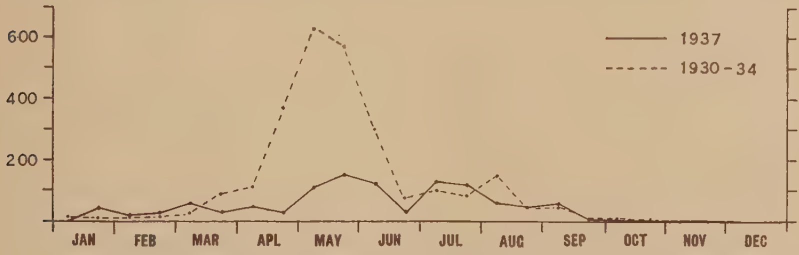


Fig. 1. Curves showing the average catches in half-hour oblique hauls with the 2-metre ringtrawl for each fortnight for all young fish, excluding clupeids, in 1937 (——) and the same averaged over the period 1930–1934 inclusive (-----).

The results for 1937 are almost a repetition of those for 1936. Once more there was an almost complete absence of the usual peak of the young of spring spawners and there were again slightly higher numbers of the young of summer spawners. The sum of the monthly average catches of those post-larvae which show maximal abundance in the months June to October inclusive, excluding clupeids, was 174 in 1937 as against 115 in 1936. These numbers were mainly made up by *Arnoglossus* sp., *C. trachurus*, *C. rupestris*, *S. scombrus*, and *B. gattorugine*. There thus appears to be a gradual swing over to better conditions for summer spawners in contrast to spring spawners the significance of which is not yet apparent.

The sums of the average monthly catches of the more important species for the year 1937 divided by the corresponding average sums for the period

1930–1934 inclusive are given below. In the second column are the figures for the best year divided by the worst year from 1930 to 1937 inclusive.

	1937 / Av. 1930–34	Best / Worst
G. merlangus	0·19	23·6 ('32/'36)
G. minutus	0·15	40·3 ('31/'35 & '36)
Onos spp.	0·40	13·0 ('30/'35)
Arnoglossus spp.	1·09	11·5 ('31/'35)
S. norvegicus	0·14	10·7 ('32/'37)
P. limanda	0·35	14·0 ('31/'35)
P. microcephalus	0·04	41·0 ('32/'37)
S. variegata	0·24	6·5 ('32/'37)
Callionymus spp.	0·28	3·8 ('30/'37)
S. scombrus	1·68	11·2 ('30/'35)
Gobiid spp.	0·02	119·0 ('30/'37)

The year 1937 has been the worst during the period 1930–1937 for *S. norvegicus*, *P. microcephalus*, *S. variegata*, *Callionymus* spp., and Gobiid spp. Except for *Callionymus*, however, the numbers of these species are becoming so low, even in some species reaching unity, that undue significance should no longer be placed on high values for the calculated figures for best divided by worst years.

The numbers of *Callionymus* have fallen from an average of 548 for the period 1930–1934 to only 155 in 1937. This decrease is very noticeable in the catches because young *Callionymus* usually bulk so largely that they are a characteristic feature of Plymouth plankton. But in spite of their decrease in actual numbers their proportionate representation is still 0·28 of the catches of all young fish, excluding clupeids, as compared with 0·38 for the period 1930–1934. The fact that this, the most abundant species, still forms approximately the same proportion of the young fish population indicates that the decrease in the numbers of young fish during the last few years has been due to some factor adverse to all species of fish indiscriminately. Indeed, if this decrease had been due to an overfishing of the reproducing stock it might have been expected that there would have been a corresponding increase in the proportionate numbers of the young of those species of fish which are not taken by the trawl. The gobies for instance might have benefited, whereas actually their numbers have dwindled to insignificance. This adds further support to the argument that it is the decrease in the amount of available phosphorus in the water which is the root cause of the poor survival of young fish.

In 1937 both *Arnoglossus* and *Scomber* were slightly above the average for 1930–1934, but the latter came nowhere near the high figure of 344 recorded for 1926. A noteworthy feature in 1937 was the unusual abundance of the young of *Serranus cabrilla* of which a catch of 24 was made on September 1.

The results for all species of young fish for the last eight years are summarized in Fig. 2. This figure shows the yearly averages for total young fish (excluding clupeids), for the young of summer spawners, and for total young fish less the young of summer spawners. It shows clearly how the drop in numbers after 1930 occurred first among the young of summer spawners, and that the decrease in the numbers of other species, mainly spring spawners, started later, reaching a very low level in 1935 at which it has remained while the summer spawned fish have slightly improved.

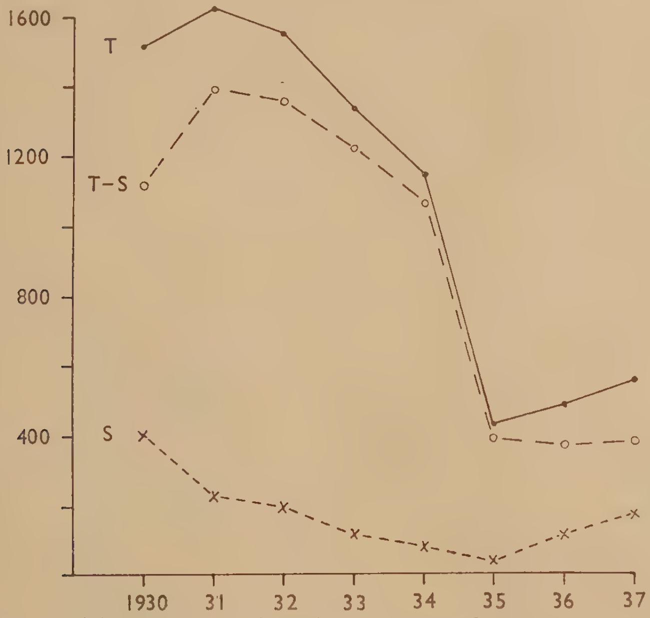


Fig. 2. The sums of the average monthly catches for each year from 1930 to 1937 in half-hour oblique hauls with the 2-metre ringtrawl for: *T*, total young fish (excluding clupeids); *S*, the young of summer spawners; and *T–S*, total young fish less the young of summer spawners.

In previous reports it was suggested that we must await a fresh inflow of water from the south of Ireland into the Channel to replenish the supply of phosphorus before there will be a return to conditions for good survival of young fish. It seemed most likely that this replenishment will come from the "elegans" water. So far there are no indications of a return to the conditions of 1930 when "elegans" water predominated off Plymouth. Figs. 3 and 4 give data on the occurrence of plankton indicators in the catches off Plymouth in 1937 in continuation of those given in the last report (1937, Figs. 2 and 3). The year 1937 was very similar to 1936. The numbers of both species of *Sagitta* were extremely low until August, when *S. setosa* became abundant, and

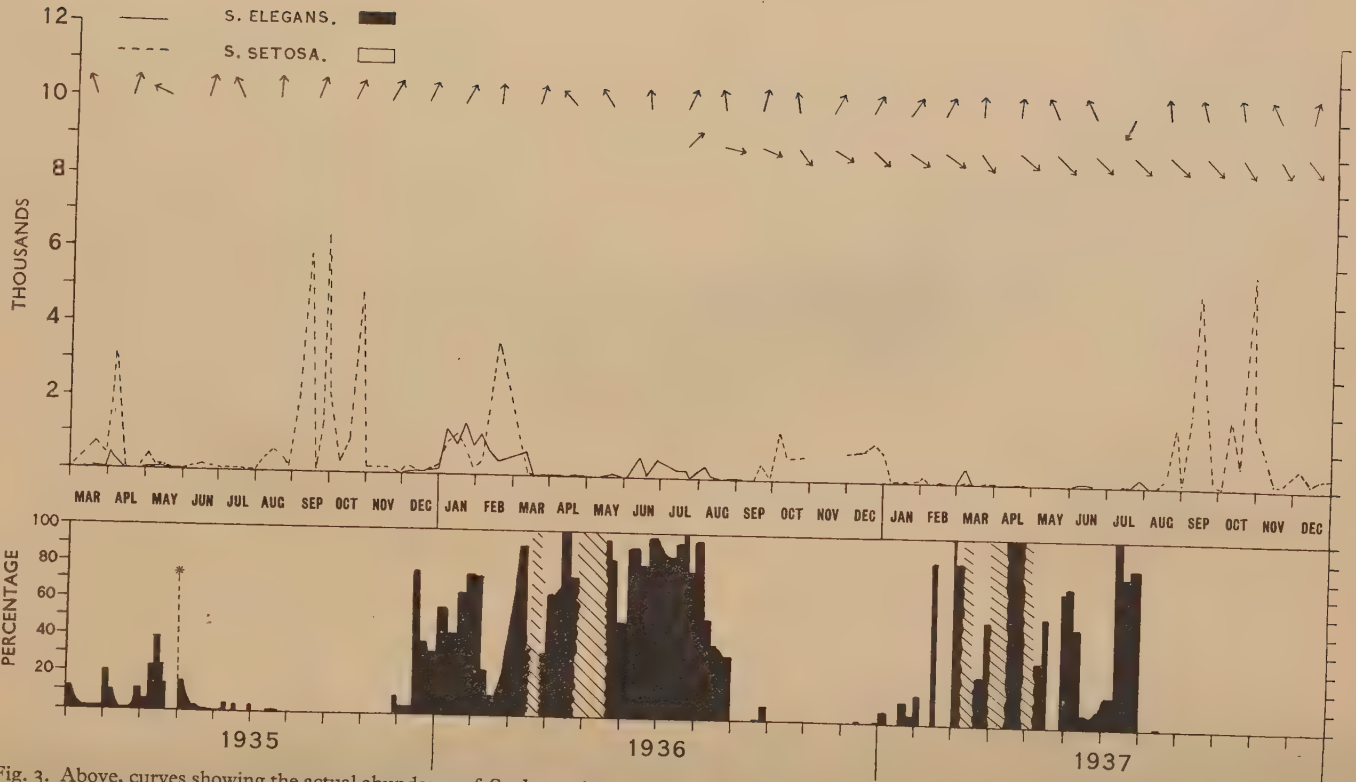


Fig. 3. Above, curves showing the actual abundance of *S. elegans* (——) and *S. setosa* (------) in half-hour oblique hauls with the 2-metre ringtrawl during the period March 1935 to December 1937.

Below, the percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagitta*, hatched.

At the top of the diagram the arrows indicate the mean directions (true) of the flow of water past the Varne Lightship (above) and the Royal Sovereign Lightship (below) from data kindly supplied by Dr J. N. Carruthers. (Continued from Russell, 1937, p. 681, Fig. 2.)

what *S. elegans* there were were much fewer than in 1936. The siphonophore *Muggiaea atlantica* was again abundant in the later summer and autumn. As in 1936 the low numbers of *S. elegans* in the first half of the year were accompanied by the appearance of unusual species. On February 24 another specimen of the scyphomedusa *Discomedusa lobata* was caught and several *Pelagia* were present in April. These two species were recorded in 1936 for the first time off Plymouth. In addition, in 1937 one specimen of the copepod *Rhincalanus nasutus* was taken on February 9; this is the first time the species has been recorded off Plymouth. It is perhaps also of interest that on February 23 the *Salpa* landed a catch with many small hake.

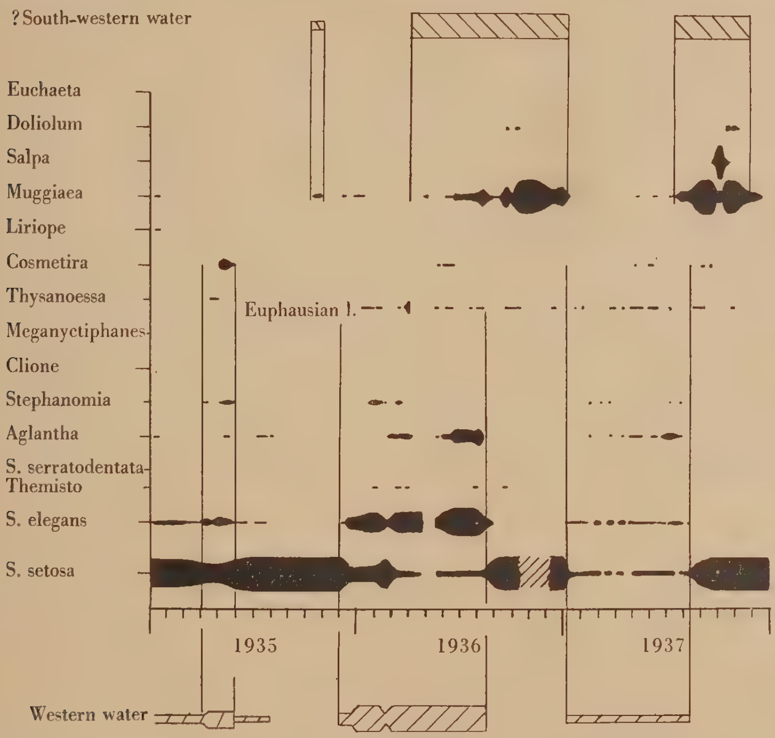


Fig. 4. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the years 1935, 1936 and 1937. (Continued from Russell, 1937, p. 682, Fig. 3.)

The *Muggiaea* species were *M. kochi* up to January 1937, and thereafter *M. atlantica*, the salps were *S. fusiformis*, and the doliolids *D. nationalis*.

On September 20 *Salpa fusiformis* appeared in the catches and had disappeared by October 19. Although the salps were not found off Plymouth on

September 13 they were present on the next day off Looe. This is the first appearance of salps off Plymouth since 1932.

As in 1936 also, pilchard eggs were a distinct feature in the plankton in 1937. They were present continuously from April to December, the approximate numbers on the different dates being as follows: April 14 (280), 26 (2320); May 3 (2360), 10 (37, 300), 19 (1000), 24 (2800), 31 (4200); June 6 (480), 14 (30,000), 18 (19,220); July 5 (14,960), 13 (7920), 19 (few), 26 (few); August 4 (1220), 11 (880); September 1 (1000), 7 (few), 13 (few), 20 (few), 27 (90); October 4 (100), 11 (320), 26 (few); November 1 (2420), 8 (300), 15 (670), 19 (20); December 6 (4), 13 (1), 31 (11).

The continuous appearance of such large numbers of pilchard eggs under conditions when the numbers of both *S. elegans* and *S. setosa* are conspicuously low deserves special mention, as it appears possible that we have here a body of water distinct from either of those characterized by the presence of *S. elegans* or *S. setosa*. If this be so, or whatever be the origin of this water, it is proposed that it should for the time being be called "pilchard" water, since it is evident that it is well worth watching in the future for the conditions that favour this great production of pilchard eggs off Plymouth.

In spite of the large number of eggs there are no indications in the ring-trawl catches that the young were abnormally abundant. The possibility that the low numbers of *S. setosa* may also be owing to their poor survival must not be lost sight of, but we do not know how abundant they were in the eastern half of the Channel.

REFERENCE

Russell, F. S., 1937. The seasonal abundance of the pelagic young of teleostean fishes in the Plymouth area. Part IV. The year 1936, with notes on the conditions as shown by the occurrence of plankton indicators. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 679–86.

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1937

All 2 miles east of Eddystone unless otherwise stated

Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
6*	2	1	6	3	6	5	4	1	4	1	6
12*	9	8	14	10	14	13	11	7	11	8	13
20	16	19‡	19§	18	18	19	18	13‖	19	15	20
27†	24	23	26	24		26	25	20	26	19¶	31
		30		31				27			

* L4–L5.
† Bolt E × S: Stoke Pt. N.
‡ L3–L4.
§ Off Revelstoke, 25 fathoms.
‖ 4–5 miles south of Breakwater.
¶ 3 miles west of Rame.

TABLE II. AVERAGE MONTHLY CATCHES OF POST-LARVAE PER HALF-HOUR

Oblique hauls with 2-metre Ringtrawl, 1937

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total Young Fish	37	116	430	56	182	150	207	60	40	40	9	1	1328
Ditto, less Clupeids	21	22	39	36	132	89	124	53	36	2	2	1	557
All Clupeid spp.	17	94	391	20	50	58	83	7	5	39	6	1	771
Clupea harengus	3	1	1	..	..	..	..	..	..	..	..	..	5
Gadus pollachius	..	..	+	1	+	+	..	..	..	..	..	..	1
Gadus merlangus	..	..	2	5	21	7	2	..	..	..	..	..	37
Gadus minutus	..	..	10	2	1	1	+	..	..	..	..	..	14
Gadus luscus	..	+	+	..	1	+	+	+	..	+	1	1	3
Gadus callarius	..	+	..	..	..	..	..	..	..	..	..	..	+
Onos spp.	..	..	1	1	13	3	2	1	..	..	..	..	21
Molva molva	..	..	..	..	+	..	..	..	..	..	..	..	+
Merluccius merluccius	..	..	..	..	..	..	..	+	..	+	..	..	+
Raniceps raninus	..	..	..	..	..	..	+	..	..	..	..	..	+
Capros aper	..	..	..	..	..	..	..	1	+	..	..	..	1
Zeus faber	..	..	..	..	..	..	..	..	..	+	..	..	+
Arnoglossus spp.	..	..	..	..	..	+	17	9	10	+	..	..	36
Rhombus spp.	..	..	..	..	..	+	2	3	2	..	..	..	7
Scophthalmus norvegicus	..	..	..	..	3	4	1	..	..	..	..	..	8
Zeugopterus punctatus	..	..	..	+	1	..	..	..	..	..	..	..	1
Zeugopterus unimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Pleuronectes limanda	..	..	+	6	9	4	..	..	..	..	..	..	19
Pleuronectes flesus	..	..	+	1	..	..	..	..	..	..	..	..	1
Pleuronectes microcephalus	..	..	..	..	+	1	..	..	..	..	..	..	1
Solea vulgaris	..	..	1	2	..	..	..	..	..	..	..	..	3
Solea variegata	..	..	..	3	7	8	1	1	..	..	..	..	20
Solea lascaris	..	..	..	..	..	..	..	..	+	..	..	..	+
Solea lutea	..	..	..	..	+	..	+	..	..	..	..	..	+
Serranus cabrilla	..	..	..	..	..	..	..	+	5	..	..	..	5
Caranx trachurus	..	..	..	..	..	..	3	8	6	+	..	..	17
Mullus surmuletus	..	..	..	..	..	..	..	+	..	..	..	..	+
Morone labrax	..	..	..	..	..	..	..	..	..	..	..	..	..
Ammodytes sp.	21	21	23	4	..	..	3	3	1	..	1	..	77
Ammodytes lanceolatus	..	..	..	1	4	3	1	1	..	..	..	..	10
Cepola rubescens	..	..	..	..	..	..	1	..	1	..	..	..	2
Callionymus spp.	..	..	..	10	69	46	12	15	2	+	1	..	155
Labrus bergylta	..	..	..	..	..	+	..	..	..	..	..	..	+
Labrus mixtus	..	..	..	..	..	+	..	..	..	..	..	..	+
Ctenolabrus rupestris	..	..	..	..	..	3	17	1	..	..	..	..	21
Crenilabrus melops	..	..	..	..	..	..	2	..	..	..	..	..	2
Centrolabrus exoletus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trachinus vipera	..	..	..	..	..	..	2	2	2	..	..	..	6
Scomber scombrus	..	..	..	..	5	24	5	3	..	..	..	..	37
Gobius spp.	..	..	..	..	+	+	1	..	+	..	..	..	1
Lebetus scorpioides	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius ocellaris	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius pholis	..	..	..	..	..	1	2	..	..	..	..	..	3
Blennius gattorugine	..	..	..	..	..	3	33	+	+	..	+	..	36
Chirolophis galerita	..	1	..	..	..	..	..	..	..	..	..	..	1
Agonus cataphractus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trigla spp.	..	..	..	..	..	+	+	..	..	..	..	..	+
Cottus sp.	+	+	2	1	..	+	..	..	..	..	..	..	3
Liparis montagui	..	..	..	..	..	..	..	..	..	..	..	..	..
Lepadogaster bimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Lophius piscatorius	..	..	..	+	..	+	..	..	..	..	..	..	+

THE ECOLOGY OF THE TAMAR ESTUARY

I. INTRODUCTION

By P. H. T. Hartley, B.Sc. and G. M. Spooner, M.A.
From the Plymouth Laboratory

(Plate XVIII)

During 1936 and 1937 extensive physical and faunistic studies of the Tamar Estuary were made by several workers at the Plymouth laboratory. These investigations, though conducted independently and with different immediate aims, proved to have considerable bearing on one another, and each worker benefited by occasions for co-operation. As the work proceeded it became clear that one of the most important aspects of each investigation was the bearing it had on the balance of life in the estuary as a whole. It was decided to publish the results of these studies in a series of papers in which each contributor should lay due emphasis on data having possible bearings on the problems studied by the others, so as to present as complete a picture as possible.

Studies have been made of salinity, temperature, penetration of daylight, macro- and micro-fauna of the intertidal zone, the sessile flora and fauna of the buoys, the fishes and their food, and the birds which frequent the flats and channels. Other studies are contemplated. In the work on light penetration and on quantitative estimates of the fauna of the mud-flats, no comparable data have hitherto been procured in this country.

The Tamar is the largest of the rivers which flow into the west end of Plymouth Sound. It is tidal for nearly 19 miles (30 km.) of its course. Rather over 3 miles (5·5 km.) from the sea it is joined by the River Lynher to form the Hamoaze, an estuary common to the two rivers. About 6 miles (9·5 km.) from the sea it is joined by its main tributary, the River Tavy. The Tamar flows over geological formations of Devonian and Carboniferous slates, shales, and grits. The Tavy flows over the same formations but rises among the peat bogs overlying the Dartmoor granite. The Lynher and its tributary, the St Germans River, also rise on granite, but they run for most of their length over Carboniferous rocks.

Estuarine Deposits

Among the more conspicuous features of the whole estuarine area are the mud-flats, often of considerable extent, which border the river channel. Mud has been so extensively deposited as to constitute the predominating element of the bottom in the intertidal zone. Even in the lower reaches of the estuary the deposits extend well up into the high-water zone, impregnating the "shillet" or stony ground which is characteristic of long stretches of shore-line. There is a marked contrast with the conditions in the Kingsbridge Estuary, where a zone of clean stones and gravel, bearing rich growths of algae, extends down to below high-water neaps. In the Tamar and its branches rocky outcrops clear of silt at the higher levels are relatively infrequent, but occur as far up the river as Neal Point. As the river mouth is approached the mud deposits do not give place to sand, as in neighbouring estuaries such as the Erme and Avon.

As may be seen on the accompanying plan (Plate XVIII), the intertidal areas occupy a large fraction of the estuary bed, and by far the greater part of these consist of the deposits referred to. They fill all the inlets and irregularities in the contours of the shore-line, tending to confine the main flow of the river and tidal streams to a central channel. Owing to their large area and to the abundance of the fauna for which they provide a habitat, these mud-banks acquire considerable importance in the ecology of the estuary; and while it would be out of place here to enter into details of their physiography, certain general features may be pointed out.

It may be noticed that the contours of the mud-banks are rarely such that a cross-section of the estuary bed shows an even decrease of level from the shore towards mid-channel; the banks tend to flatten out and acquire a steeper slope on their outer face. The levelling process has often gone so far that in any place a large proportion of the surface of the mud-bank will lie between certain narrow limits of vertical height. Since change in vertical height implies change in the amount of exposure to the air on the ebb tide, or of exposure to varying salinities on the flood, this factor is important in faunistic studies. For brevity we may refer to those regions of the mud-banks where the gradient is at a minimum as "flats". As a general rule not only do the flats include a considerable fraction of the total area of a bank, but also, as they are apparently usually subjected to least disturbance from currents, they provide the most favourable habitat for the mud fauna. Consequently it is important to note, in any area, the levels at which the flats occur.

In the first place it emerges that though, where the estuary is broad, the flats may extend well below the permanent water channel (as off West Muds, and at the junction of the Tavy), they are more usually mainly or entirely intertidal. Secondly, as the estuary is ascended, and as the rock bed of the estuary rises, so rises the average level of the mud-flats. One effect of this is that an increasing proportion of the intertidal zone is uncovered at half-tide. In many places the approximate level of the half-tide line has been ascertained and is shown on the plan (Plate XVIII). Both the estuaries of the Tamar and Tavy above their junction show this phenomenon fairly diagrammatically, while smaller branches such as St John's Lake and Millbrook Lake provide excellent examples in miniature. Above a certain point the area between half-tide and the channel comprises a nearly uniform narrow zone with a relatively steep gradient; while the greater part of the mud-bank lies above, with a lesser gradient which varies with the breadth of the tidal zone. A great proportion of the fauna of these mud-banks is thus saved from the low salinities which prevail on the ebb tide. Also, as the river is ascended, birds have increasing opportunities over fish as predators of the mud fauna.

Another aspect of the up-river rise of the level of the mud-banks is that, unless currents interfere, mud is more freely deposited near high-water springs. As a result the substratum in the zone between high-water springs and neaps becomes increasingly favourable, where the gradient permits, for the development of saltings. The salting flora, of which *Salicornia* is the pioneer, is able to establish itself on flat stretches below the level of ordinary tides, where it is uncovered for no more than two or three consecutive days. Up river all the flatter (and so broader) ground between ordinary high water and springs is occupied by saltings. It is common knowledge that once saltings have become established they accelerate the deposition of silt, and so rise more rapidly than the adjoining areas of clear mud. At the same time erosion of the edges produces an increasingly abrupt transition line between the clear mud and the salting, the boundary of which comes to be marked by a "salting cliff". Various stages in this process may be seen passing from Salt Mill to Egypt Salt Marsh to Clifton. In the latter vicinity the salting cliff attains the height of 1 m. In the upper reaches of the estuary the top of the salting cliff approximately coincides with the level of ordinary tides (+1·7 m. O.D.). The greater part of the saltings on the Tamar above Cargreen, and on the Lynher above Sheviock Wood, are uncovered for the whole week of neap tides.

Saltings tend to fill up all the irregularities in the contours of the spring-tide shore-line. This natural, but slow, process of land reclamation has in some places been completed artificially by the construction of embankments and drainage ditches (at Landulph, on the north side of Kingsmill Lake; and opposite Pentillie). A large inlet cut off by Ernesettle railway embankment has also been reclaimed during the past century.

In the upper reaches the river is in many places bounded by steep slopes. The mud-banks here are narrower, but still show an increasing gradient on their outer face. For considerable stretches steep hanging woods extend to the river's edge. In winter great quantities of sodden leaves accumulate in the river, and are deposited in the mud on the inner sides of curves near low-water mark, as well as along the channel in deeper water.

When a winter flood is beginning to decrease a layer of fine, sticky, grey mud, locally called "slurry", is deposited on the flats, and lies there until scoured away by the next spring tides. This may be responsible for temporary fluctuations in the level of certain flats.

In general the mud-banks appear to have considerable stability, and their growth, below the level of saltings at least, appears to be extremely slow. It is difficult to detect any appreciable changes during recent years. Signs of growth might be expected in a situation such as the east shore above Saltash, where a railway embankment raised from a level lying below half-tide has provided a new shore-line. The survey of a traverse in 1937 can be compared with the Admiralty Chart surveyed in 1894. Though a significant difference is found, it cannot be considered great. The bank appears to have risen nearly a metre in the centre, but scarcely at all on the face of the embankment. The result is that the bank rises somewhat more steeply from the river, is more level on its main expanse, but still remains well below the half-tide level.

The consistency of the mud deposits may be described as "soft", as contrasted with that of stiffer muds which contain a large admixture of fine sand. Progress over the banks is often difficult, a man usually sinking above the ankles at each step, and often to the knees. Surface samples from different situations vary most in the materials which are mixed with the silt. Valves of mollusc shells are almost always present, sometimes comprising the main bulk of the deposit. Vegetable residues ranging from very finely divided shreds to whole leaves and pieces of twig are always present, though in extremely variable quantities. But there is a marked absence of admixture of sand particles, and gravel is only obtained from sievings of samples taken near high water in the lower reaches. Thus the more solid components of the mud deposits consist almost entirely of valves of mollusc shells and their fragments. *Cardium edule*, *Scrobicularia plana*, *Peringia ulvae*, and *Littorina littorea* are the main species concerned. Their abundance is sometimes such that they form a conspicuous feature of the landscape, as they lie thickly strewn on the surface of the flats, or accumulated in a mass along the course of drainage channels.

DEPTH OF THE CHANNEL AND TIDAL RANGE

In the harbour area (Hamoaze) the river channel attains a considerable depth, attaining 37·8 m. (124 ft.) near Devil's Point. The depth steadily decreases northward. Beyond 5 km. from the mouth only two small depressions exceed 15 m. (49 ft.). The Lynher shallows to a maximum of 5 m. at the point where it widens, and to the order of 1 m. at Sheviock Wood. The main river shallows rapidly above Saltash Bridge, and above the junction of the Tavy only just exceeds 5 m. in two places. At Cargreen there is a slight indication of a decrease in average tidal fall (see Table II), but this does not become pronounced until the bend in the river above Clifton. However, at Pentillie Quay, 16·5 km. from the mouth, it is only 0·62 m. less than at Devonport. The subsequent rise of the river bed relative to sea-level is very gradual in the winding Tamar, and the influence of the tide does not die out until 30 km. from the mouth. The bed of the Tavy, however, rises much more quickly. Even at Bere Ferrers it has apparently risen above Chart datum. Tidal influence soon disappears after the narrowing of the river at Lopwell, at some 17 km. from the mouth.

The depth of the channel in the harbour area ensures a strong tidal scour of the lower reaches of the estuary, and checks the encroachments of the mud-banks. Dredging operations help in the same direction, and there has apparently been little change in the bed of the Hamoaze in recent years. However, from the junction of the Lynher to Saltash an appreciable shallowing has taken place. In the upper reaches, too, the local watermen say the channel is becoming shallower. They attribute this to the fact that small paddle steamers no longer run between the villages along the shores. The churning of the paddle wheels may well have artificially affected the depth of the channel at some points, but noticeable changes subsequent to the removal of this influence are more likely to involve a return to a normal equilibrium than a renewal of a progressive silting.

The data relating to the tide levels are given in Table I. It will be observed that the mean range of tide is 4·73 m. (15·52 ft.) for spring tides, and 2·34 m. (7·65 ft.) for neaps, extremes in 1937 being 5·55 and 1·44 m. respectively. Table II gives the relative tidal range at seven positions in the tidal area, following the Channel Pilot.

TABLE I. TIDAL LEVELS AT DEVONPORT IN RELATION TO ORDNANCE SURVEY DATUM

	Metres	Feet
Highest predicted tide 1937	+2·53	+8·3
Mean high-water springs	2·22	7·28
Mean high-water ordinary tides*	1·70	5·58
Mean high-water neaps	1·17	3·83
Lowest predicted high tide 1937	0·70	2·3
Mean sea-level	0·22	0·73
Land Survey (Ordnance) Datum	0·0	0·0
Mean tide, Devonport	−0·08	−0·27
Highest predicted low tide 1937	−0·77	−2·52
Mean low-water neaps	−1·165	−3·82
Mean low-water ordinary tides*	−1·82	−6·00
Mean low-water springs	−2·51	−8·24
Admiralty Datum	−2·566	−8·42
Lowest predicted tide 1937	−3·02	−9·9

* The high- and low-water contours are inserted on the plan (Plate XVIII), following the practice of Ordnance maps.

TABLE II. RELATIVE TIDAL RANGES AT SPRINGS

Position	Distance from mouth in km.	Tidal range	
		Metres	Feet
Devonport Dockyard	3	4·7	15·5
Saltash, River Tamar	6·8	4·6	15·0
Cargreen, River Tamar	11	4·5	14·75
Pentillie, River Tamar	16·5	4·1	13·5
Calstock, River Tamar	22	3·8	12·5
Warleigh Quay, River Tavy	10·5	4·4	14·5
Maristow, River Tavy	14	2·6	8·5

There is considerable eddying of the tidal stream within the river. Close inshore there is a current running in the opposite direction to the set of the tide—the so-called "eddy tide". When much fresh water is coming down, the flood tide will move up on one side of the river before its influence reverses the direction of the surface flow upon the other. The two bodies of water may be distinguished by the line of floating leaves and debris where they meet and by the muddiness of the fresh water. The upward flow of the rising tide is first felt along the bottom of the river.

A southerly gale will choke back the tide in the estuary so that the water level at the slack of the ebb may be several feet above that predicted. When the next rising tide drives in before the storm, considerable flooding may take place. A northerly gale will cause a stronger ebb than usual and a depression of high-tide level.

The greatest speed of the tidal stream within the harbour is 2¾ knots (Channel Pilot).

RAINFALL

Along the valleys of the Tamar and its tributaries the mean annual rainfall is from 950 to 1150 mm. per annum: but the drainage area lies between two of the wettest places in the west of England—Dartmoor and the Cornish moors. At Princetown, on Dartmoor, the normal rainfall is 2079 mm. per annum, and at Altarnun on the Cornish side, 1503 mm. In Table III is shown the rainfall at Plymouth near the mouth of the river (normal annual rainfall: 933 mm.) and at Princetown.

TABLE III

	Plymouth			Princetown		
Months	Normal	1936	1937	Normal	1936	1937
Jan.–Mar.	233	388	431	568	612	941
Apr.–June	166	87	189	339	218	332
July–Sept.	213	254	126	439	622	324
Oct.–Dec.	321	199	304	733	604	411

During the first three months of both years the rainfall was greatly in excess of the normal. In July 1936, the rainfall was greater than normal and floods of thick, brown water came down from the moors. The rest of the summer of 1936 and the summer of 1937 were drier than usual.

HUMAN ACTIVITIES

A small and diminishing population of fishermen work in the estuaries of the Tamar and Lynher. Large seines for salmon and sprats are used, and a modified shore-seine, the "Saltash Tuck Seine", is used for the capture of flatfishes. In the autumn, herrings are caught in drift-nets. Motor boats from Plymouth trawl for prawns in the harbour area, and some shrimps and prawns are taken in hand-nets during the summer. On the flats of West Muds winkles and cockles are gathered; cockle beds outside Skinham Creek are also picked over occasionally. Mussels from the river are not saleable, and the oyster beds (near Saltash) are worked out. After December 1937, the sale of all shellfish from the estuaries was prohibited by the local medical authorities. Only one professional punt-gunner now works in these waters, and there is very little shore-shooting. Above Hole's Hole rotten leaves are collected from the flats for use as manure.

The eastern side of the Hamoaze from Devil's Point to Bull Point is covered by the quays and buildings of Devonport Dockyard. There is no pollution of the rivers by commercial effluents. A number of sewers release crude sewage into the channels: much of this matter is at once eaten by the mobs of gulls which haunt the outfalls. Unlike certain other rivers which flow off Dartmoor and the Cornish moors, those in this watershed never carry the milky white suspension derived from China-clay washings. Pollution by crude oil residues, as far as it can be determined by the presence of oiled sea-birds or stranded clots, is not found in the estuary. Small quantities of lighter oils are constantly being discharged in the harbour area from motor-driven vessels, but it is extremely questionable whether these have any harmful effects, and even if proof of such is ever obtained, the extent to which it occurs is very probably negligible.

PREVIOUS BIOLOGICAL WORK

Duncker (1899) made a statistical examination of flounders caught in the Tamar. Ford (1928) fished for young herring with a small-meshed seine-net in the Tamar, Tavy, and Lynher, and published his results in the fourth paper of "Herring investigations at Plymouth". In 1929 Percival published the results of an investigation of the fauna of the Tamar and Lynher, carried out between June and November, 1928. The paper contains a description of the area, an annotated faunistic list, and some observations on salinity variations. Percival points out that 1928 was an unusually dry summer. Certain analyses of his data are made in the Survey of the River Tees, Part II (pp. 79–81). After Serventy (1935) had recorded the occurrence of *Gammarus zaddachi* in the Tamar, Crawford (1937) made a more detailed study of the distribution of certain Crustacea (Tanaidacea, Isopoda, and Amphipoda) in the estuarine zone of the three main rivers. Moore's studies on the biology of *Balanus* (1936) and *Littorina littorea* (1937) deal with populations of these animals from Henn Point and Treval respectively.

Note

In the spelling of place-names we follow the Ordnance Survey, but it should be pointed out that for some names alternative spellings are still in use. Thus Neal Point is variously "Neil" (Admiralty Chart) or "Neille" (Percival, 1929; Crawford, 1937). Another locality appears to be "Treval" or "Trevol", according as it is approached from the land or the water! There are names such as Warren Point which recur in this and other estuaries with inconvenient frequency, and care should be employed in their use. In Crawford's map (1937, p. 649) the names Bull Point and Weston Mill Lake are misplaced.

Various information, such as depths, has been derived from the following

Admiralty Charts: Plymouth Sound and Hamoaze, surveyed 1898–9, with large corrections to 1931, and small corrections to 1937; Tamar River (Saltash to Cargreen), surveyed 1894, with additions to 1905; entrance to St Germans or Lynher River, surveyed 1923, with small corrections to 1937.

The information given here on intertidal levels, e.g. the half-tide line, is based on the survey of certain traverses made in 1936–7, supplemented by observations on the state of the tide in a general view of stretches of estuary, at the appropriate time and in suitable weather conditions. No great exactness is claimed.

REFERENCES

Admiralty Tide Tables, for 1937 and 1938. H.M. Stationery Office, London. 1936 and 1937.

Alexander, W. B., Southgate, B. A., and Bassindale, R., 1935. Survey of the River Tees. Part II. The Estuary—chemical and biological. *D.S.I.R. Water Pollution Research*, Tech. Paper No. 5, H.M. Stationery Office.

Channel Pilot, Part I. Ninth edition. Admiralty. 1900.

—— Twelfth edition. Admiralty, 1931. With Supplement No. 5, including corrections to November 10 1937.

Crawford, G. I., 1937. The fauna of certain estuaries in west England and South Wales, with special reference to the Tanaidacea, Isopoda, and Amphipoda. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 647–62.

Duncker, G., 1899. Variation und Asymmetrie bei *Pleuronectes flesus* L. *Wiss. Meeresuntersuch. Abt. Helgoland*, Bd. iii, pp. 333–406.

Ford, E., 1928. Herring investigations at Plymouth. IV. The growth of young herrings in the neighbourhood of Plymouth. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 305–19.

Meteorological Office. 1924. *The Book of Normals of Meteorological Elements for the British Isles for Periods ending* 1915. Section V.

Moore, H. B., 1936. The biology of *Balanus balanoides*. V. The distribution in the Plymouth area. *Journ. Mar. Biol. Assoc.*, Vol. xx, pp. 701–16.

—— 1937. The biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life and mortality. *Journ. Mar. Biol. Assoc.*, Vol. xxi, pp. 721–42.

Percival, E., 1929. A report on the fauna of the estuaries of the River Tamar and the River Lynher. *Journ. Mar. Biol. Assoc.*, Vol. xvi, pp. 81–108.

Serventy, D. L., 1935. Observations on *Gammarus zaddachi* Sexton, an estuarine amphipod, and associated forms. *Int. Rev. Hydrob. Hydrogr.*, Vol. xxxii, pp. 285–94.

PLAN OF THE TAMAR ESTUARY BASIN

The *Intertidal zone* between *Ordinary High and Low Water* marked in fine stipple.

Saltings indicated by coarse irregular stippling.

Only the main streams through the intertidal zone are inserted. Ramifying channels through saltings are omitted. Fresh-water streams flowing into the estuary are not traced to their source.

The dotted line dividing the intertidal zone represents *the approximate position of half-tide* where this has been ascertained.

Contours in the permanent channel are given at intervals of 5 m. depth below Admiralty datum. The deeper part of the channel exceeding 15 m. (approximately 8 fathoms or 50 ft.) is blackened.

The course of the main river, the Tamar, is marked in *kilometre intervals* from the mouth (zero position at the level of Devil's Point).

Certain *mooring buoys* from Plymouth Sound to Saltash are marked as follows. *D* 1 *to* 4: Drake's Island Buoys. *Cr. By.*: Cremyll Buoy. *H* 1 *to* 15: Hamoaze Buoys, Nos. 1 to 15.

The plan is orientated (2° W. of N.) with respect to the Ordnance Survey National Grid, of which 1000 yard intervals are marked along the border. The lower section covers 820·5–833·66 (thousand yards) E. and 166·86–174·06 N. The upper section covers 825·1–833·66 E. and 173·57–181·5 N.

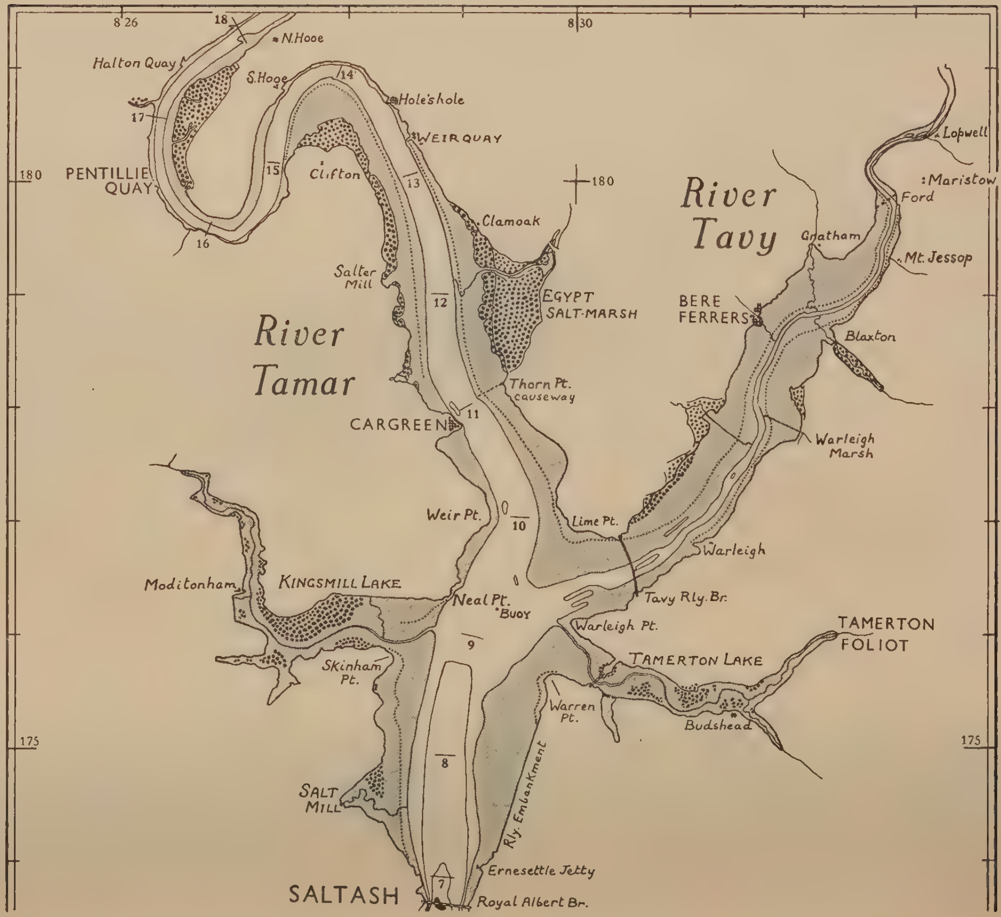
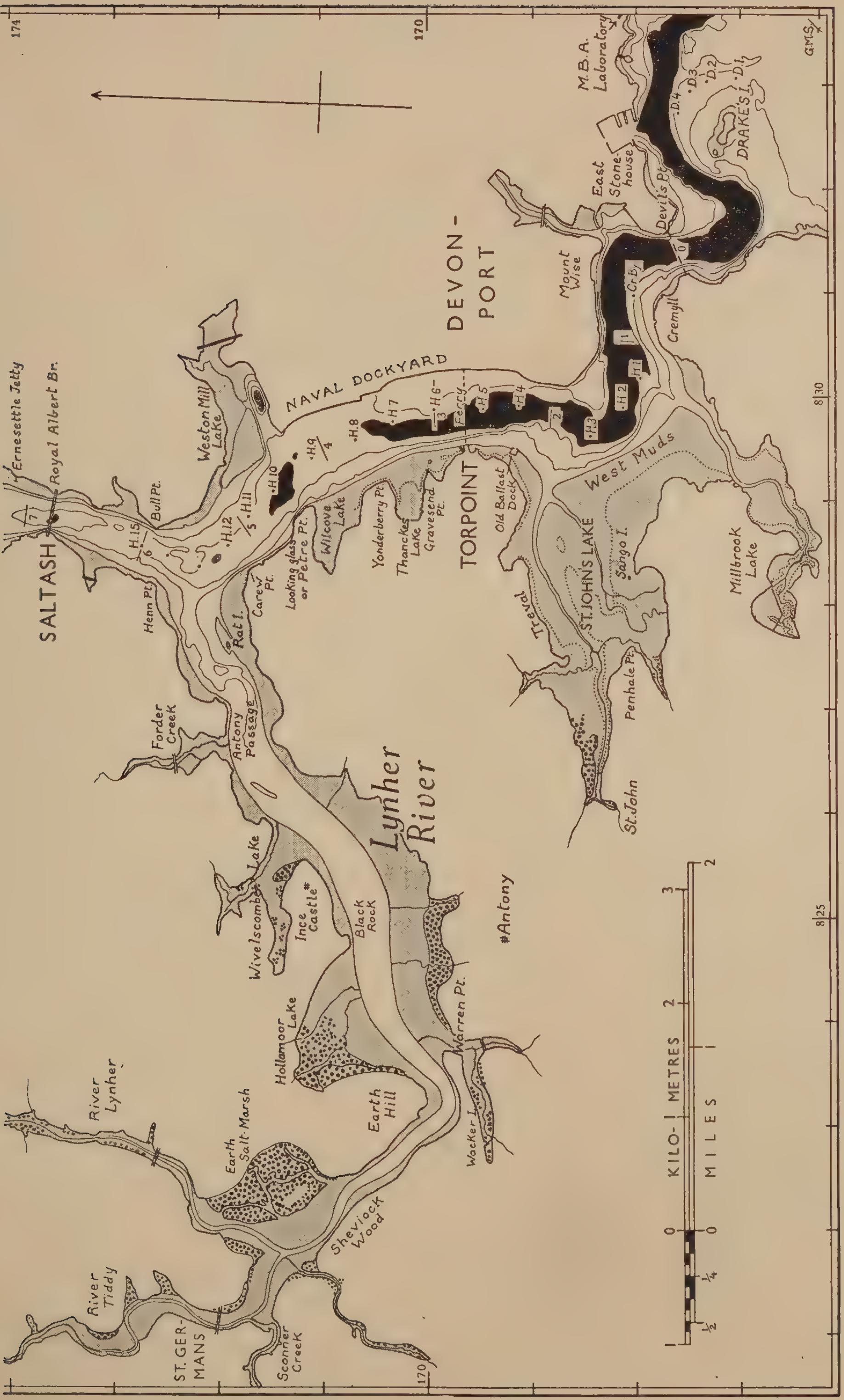

8 26
8 30
180
175
18
17
16
15
14
13
12
11
10
9
8
7
N.Hooe
Halton Quay
S.Hooe
Hole's hole
WEIR QUAY
PENTILLIE QUAY
Clifton
Clamoak
Salter Mill
EGYPT SALT-MARSH
River Tamar
Thorn Pt. causeway
CARGREEN
River Tavy
Lopwell
Maristow
Ford
Mt. Jessop
Gnatham
BERE FERRERS
Blaxton
Warleigh Marsh
Lime Pt.
Warleigh
Weir Pt.
Tavy Rly. Br.
Moditonham
KINGSMILL LAKE
Neal Pt.
BUOY
Warleigh Pt.
TAMERTON FOLIOT
TAMERTON LAKE
Skinham Pt.
Warren Pt.
Budshead
Rly. Embankment
SALT MILL
Ernesettle Jetty
SALTASH
Royal Albert Br.

PLATE XVIII


174
170
170
8|30
8|25
G.M.S.
M.B.A. Laboratory
D.1
D.2
D.3
D.4
DRAKE'S I.
East Stonehouse
Devils Pt.
DEVON-PORT
Mount Wise
Cr.By
0
1
Cremyll
H.1
H.2
H.3
2
NAVAL DOCKYARD
H.4
H.5
H.6
3
Ferry
H.7
H.8
H.9
4
H.10
H.11
5
H.12
H.15
6
7
Ernesettle Jetty
Royal Albert Br.
Weston Mill Lake
Bull Pt.
SALTASH
Henn Pt.
Carew Pt.
Looking glass or Petre Pt.
Wilcove Lake
Yonderberry Pt.
Thanckes Lake
Gravesend Pt.
TORPOINT
Old Ballast Dock
West Muds
ST. JOHNS LAKE
Sango I.
Millbrook Lake
Treval
Penhale Pt.
St. John
Rat I.
Forder Creek
Antony Passage
Lynher River
Wivelscombe Lake
Ince Castle
Black Rock
Antony
Hollamoor Lake
Warren Pt.
Earth Hill
Wacker L.
River Lynher
Earth Salt-Marsh
Sheviock Wood
River Tiddy
ST. GERMANS
Sconner Creek
KILO-METRES
0
1
2
3
MILES
0
¼
½
1
2

THE ECOLOGY OF THE TAMAR ESTUARY
II. UNDER-WATER ILLUMINATION

By L. H. N. Cooper, Ph.D., F.I.C. and A. Milne, M.A., B.Sc.
From the Plymouth Laboratory

(Text-figs. 1–6)

Studies on illumination in the waters of the open sea made from this and other laboratories (cf. Atkins & Poole, 1933) have stressed the profound effects of varying transparency of sea water upon plant growth. Therefore during ecological investigations in the Tamar Estuary or Hamoaze, some measure of the light available for plants growing on the banks and in midstream on mooring buoys was sought. For work in shallow turbid water, the photo-electric method has certain disadvantages due to shading by the boat and the necessity of measuring the depth of the cell on a scale of centimetres rather than of metres. Steemann Nielsen (1935) has used the Zeiss Pulfrich photometer for measuring the extinction coefficients of blue and green light in Icelandic waters. For measuring the turbidity of North Sea water Kalle (1937) also has used this photometer in combination with the red S 72 light filter. In the present investigation the photometer has been used for measuring the transmission of light throughout the visible spectrum. The results can be linked up with photo-electric measurements.

METHOD OF MEASUREMENT

The photometer measures directly the absorption or extinction coefficient of a coloured or turbid solution compared with distilled water; 0·25 m. twin absorption tubes have been employed. As commonly used the distilled water tube serves to give a balanced optical system and to eliminate from the measurement the undesired absorption by water itself, but for our purpose this absorption must be considered. When the instrument is correctly set up, the intensities of light of given wave-length entering the twin tubes, each of length d metres, will be identical, I_0, but after passing through d metres of distilled water or of sea water, the intensities will be reduced to I_1 and I_2 respectively. The following relations then hold:

$$d\mu_{DW} = \log_e \frac{I_0}{I_1}, \qquad \text{......(1)}$$

$$d\mu_{SW} = \log_e \frac{I_0}{I_2}, \qquad \text{.......(2)}$$

where μ_{DW} and μ_{SW} are the extinction coefficients of distilled water and sea water respectively for light of a given wave-length. The measurements compare the intensities of light which emerge from the tubes, that is

$$d\mu_M = \log_e \frac{I_1}{I_2}, \qquad \text{......(3)}$$

where μ_M is the extinction coefficient as measured. A simple rearrangement shows that

$$\mu_{SW} = \mu_M + \mu_{DW}. \qquad \text{......(4)}$$

The transmission curves for the eight spectral filters used are shown in Fig. 1, reproduced by permission of Messrs Carl Zeiss (Jena). In most cases the cut off is very sharp. For this investigation the S 66·6 filter was not available.

Sawyer (1931) has summarized measurements of the extinction coefficients of distilled water. His own measurements extend up to 650 mμ. and appear amongst the most suitable for our purpose. Later Dawson & Hulburt (1934) redetermined μ_{DW} in the visible spectrum between 540 and 690 mμ. (Table I). Lange & Schusterius (1932) published results for an extinction coefficient, ϵ_{DW}, defined by the equation: $x\epsilon_{DW} = \log_{10} \frac{I_0}{I_1}$, where x is measured in centimetres (see their correction redefining their coefficient). Using the relation $\mu_{DW} = 2{\cdot}3 \times 100\, \epsilon_{DW}$, their graph gives μ_{DW} as approximately 0·27, 0·18, 0·50 and 2·8 at 500, 560, 670 and 750 mμ. respectively. On many occasions throughout the visible spectrum, as far indeed as 800 mμ., considerably lower values of vertical extinction coefficients in the open sea have been found by Poole & Atkins, Utterback, and Clarke. Since the extinction coefficients of distilled water are unlikely to exceed these values, Lange & Schusterius' figures have had to be rejected. The accepted figures in Table I for the filters S 43–61 were based solely on Sawyer's data, since we had not

TABLE I. EXTINCTION COEFFICIENTS OF DISTILLED WATER, μ

Spectral filter	Wave-length at centre of gravity of filter mμ	μ		
		Sawyer (1931)	Dawson & Hulburt (1934)	Accepted value
...	400	0·072	0·08	...
S 43	440	0·023	...	0·02
S 47	460	0·015	...	0·02
S 50	490	0·015	...	0·02
S 53	530	0·021	...	0·02
...	540	0·024	0·04	...
S 57	570	0·038	...	0·04
...	589	0·082	0·14	...
S 61	620	0·178	...	0·18
...	650	0·21	...	...
...	670	...	0·34	...
...	690	...	0·39	...
S 72	*ca.* 720	...	...	0·47
S 75	*ca.* 750	...	...	0·54

then discovered Dawson & Hulburt's paper. For our purposes the differences between the two sets of measurements are too small to warrant recalculation

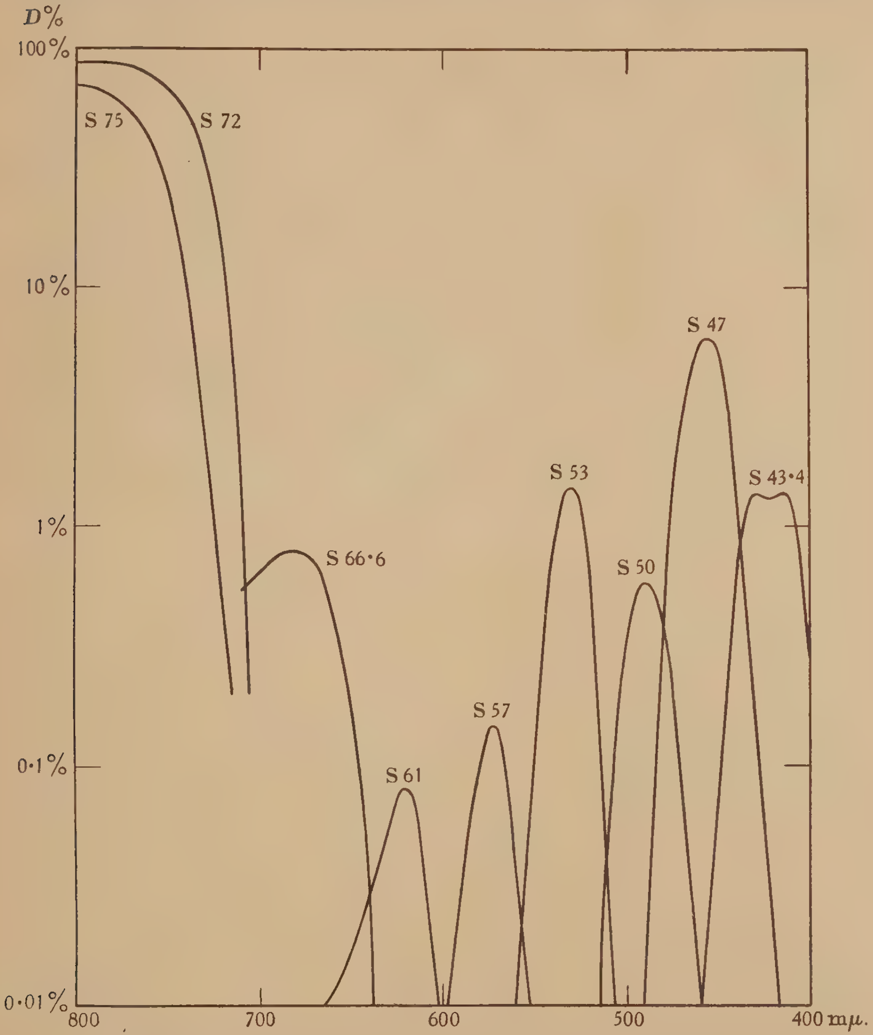


Fig. 1. Transmission curves for the spectral filters used with the Pulfrich photometer (supplied by Messrs Carl Zeiss).

of our results. The new results at 670 and 690 mμ. are of much value in arriving at the correction factors for the S 72 and S 75 filters. If, as would appear, the coefficient in this region is increasing linearly with wave-length,

μ_{DW} would be about 0·47 at 720 mμ. and about 0·54 at 750 mμ. These values have been used for the correction factors which must at present remain somewhat uncertain. Aschkinass (1895) found very high values for the extinction coefficient of pure water above 720 mμ. ($\mu_{DW} > 1$). Dr Atkins has very kindly examined for us the transmission curves of the Schott and Gen RG 7 and RG 8 filters used in his work on the transmission of red light in the sea. From his records it would seem that sea water shows nothing like such a high extinction coefficient. Thus Atkins & Poole (1933, p. 152) found vertical extinction coefficients 0·435, 0·480 and 0·567 at 660, 700 and 760 mμ. respectively. Pure water is unlikely to be more opaque than this.

Different samples of distilled water no doubt vary considerably in transparency. Our laboratory still gives water of excellent quality, so that for this investigation where the correction makes only a small change in the final value, Table I is appropriate. Should the method be used for more transparent waters, the distilled water correction would require further study.

Usually the two sides of the photometer will not be in exact optical balance. In consequence four readings with each of the eight spectral filters were made consecutively with the tube containing distilled water on the right hand. The tubes were then interchanged and a further similar series of observations made. To prevent settling of sediment, they were rotated through about 45° after every four readings. For each filter μ_M is therefore the mean of eight readings.

COMPARISON WITH THE PHOTO-ELECTRIC METHOD

Both methods give results in terms of an extinction coefficient μ defined by the equation

$$\mu = \log_e \frac{I_0}{I} \Big/ d.$$

Poole & Atkins use a quantity, μ_v, which they earlier (1926) described as the "vertical absorption coefficient" and now (1937) prefer, in agreement with Pettersson, to call the "vertical extinction coefficient"; μ_v is defined by the above equation in which d represents the difference in depth and not the unknown length of path travelled by the light. They concluded (1933) that for off-shore measurements below 10 m. with photometers limited to a restricted spectral range, μ_v as a measure of opacity is unlikely to be in error by more than a few per cent. It had been found by experiment to be practically independent of the angle of incidence at the surface.

Light passing through water may be transmitted, absorbed by the water, or absorbed or scattered by suspended solids. If a beam follows an oblique but straight path for n metres, the true extinction coefficient due to absorption only, $\mu_{n\,(absorption)} = \log_e \frac{I_0}{I_2} \Big/ n$, will be less than the vertical extinction coefficient due to absorption only, $\mu_{v\,(absorption)} = \log_e \frac{I_0}{I_2} \Big/ d$.

That part of the light scattered will become omni-directional but will not be lost unless it is reflected back out of the water. Nevertheless, in turbid water scattering will greatly increase the length of path of a ray passing downwards, so providing the opportunity for proportionately great absorption. The milky appearance of turbid water both in the estuary and in the photometer tubes shows this scattering to be considerable. If we consider a cylindrical sample of turbid water surrounded, as in the estuary, by similar water, as much light will be gained from the surrounding water by scattering as will be lost to it. For such a sample in a glass absorption tube in a dimly lit room, light incident on the water/glass surface at less than a certain angle will be completely lost from the water. If the water/glass and glass/air surfaces were plane and parallel, the limiting angle of incidence on the water/glass surface would be the critical angle for water/air, 48·5°. However, due to the curvature of the walls, the limiting angle of incidence for light not originating on, or from the direction of, the axis of the tube may be somewhat greater than this. As against this, the aperture of the measuring diaphragm receives only light which has traversed the central portion of the tube where conditions are more like those in nature, so that, although the measured extinction coefficient may be somewhat too great, due to loss of scattered light, the error is unlikely to be serious. Both methods are subject to inherent errors, but these are considered to be sufficiently small not to invalidate comparison between extinction coefficients determined by them.

Position of Observations

The exact positions examined will be found in Part I (Plate XVIII). The lowest is near the western end of Plymouth Breakwater and 2·0 km. to the N.N.E., still within Plymouth Sound, is Drake's Island No. 1 Buoy. Relative to the estuary this buoy is situated − 2·5 km. from the adopted zero line at the mouth, following the continuation of the main channel. Hamoaze No. 1 Buoy lies off Cremyll, No. 7 off Thanckes Lake, No. 15 below Saltash, and Neal Point Buoy in midstream at the junction of the Tavy, at distances of + 1·2, 3·4, 6·0, and 9·25 km. respectively from the estuary mouth.

Influence of Stratification

Observations in Plymouth Sound, even in the winter rainy season, have shown that the salinity varies little in the first metre or so below the surface. Salinity stratification increases in the up-river direction, and above Saltash bridge may become considerable during a winter spate (see Part III). In the Tamar Estuary, the maximum stratification may be expected at the upper limit examined, Neal Point Buoy. It will be shown in Part III that even in time of rainfall, equivalent to normal winter fall, the variations in salinity down to 1·8 m. are small and, for the top metre, negligible. Solid matter in suspension in an estuary arises from the inflowing river water and by tidal scouring of the muddy banks and bottom. The mixing processes are complex, but the amount of solid matter in any sample of water taken from the estuary is more or less directly dependent upon the degree of mixing of sea water with river water which, in times of spate, may be heavily laden with silt, and upon the time the various waters have spent in the estuary. Of this mixing the salinity is a measure, so that it is reasonable to suggest that waters of similar salinity carry, in general, much the same amount and kind of suspended solids. The considerable turbulence always present in isohaline water in a strongly tidal estuary would tend to keep conditions in the uppermost metre uniform. We therefore feel justified in considering our 0·3 m. samples representative of conditions down to rather more than 1 m. Whether there are more or less suspended solids at greater depths requires further investigation. In Gullmar Fjord Pettersson's observations showed that the underlying water may be much clearer but tidal forces are there much weaker than in the Hamoaze.

The relation between extinction coefficients and salinity is shown in Fig. 2 for green light measured with the S 50 filter. Below about 30°/₀₀ salinity a fair degree of inverse proportionality exists. With more saline water, in which sediment from the river has had a greater and more variable time in which to settle, no simple relation holds. The extinction coefficients for January 25, although of less accuracy than those determined later, are of much interest (Fig. 2). On this occasion silt determinations were also made by filtering 2–3 l. of estuarine water through a small tared No. 42 Whatman filter paper, washing with distilled water and drying at 100° C. to constant weight.

At the Breakwater (0·3 m.) salinity was very low, indicating a thin layer of river water spreading over the salter water beneath. This upper layer of water was associated with 5·3 mg./l. of silt and high extinction coefficients for light of all wave-lengths ($\mu_{500} = 5{\cdot}0$; $\mu_{720} = 3{\cdot}8$). Near Drake's Island the surface water was more saline and more transparent, yet carried more silt. Thence up-river to Hamoaze No. 7 Buoy, salinity, silt content and extinction coefficients varied in the way one would have forecast. Still further up-river at No. 15 Buoy, the water was still fresher but, to our surprise, contained less silt and was less opaque (Table II).

TABLE II. HAMOAZE POSITIONS, JANUARY 25 1937

	No. 1 Buoy	No. 7 Buoy	No. 15 Buoy
State of tide, hours flood	4	4·5	5
S °/₀₀	20·4	14·1	11·6
Silt, mg./l.	10·5	18·5	10·4
μ_{500}	5·1	9·0	8·4
μ_{720}	4·4	6·7	5·8

EXTINCTION COEFFICIENT

Throughout the visible spectrum the extinction coefficients in the Hamoaze (Fig. 3) are always higher, often much higher, than in the English Channel. The coefficients increase in the up-river direction and with falling tide because, first, the river is the chief contributor of suspended matter and secondly, the proportion of sea water, originally relatively clean, decreases.

In the winter of 1936–7 excessive rainfall (see Part III) saturated the watershed; most of this must have run straight off the ground into the river

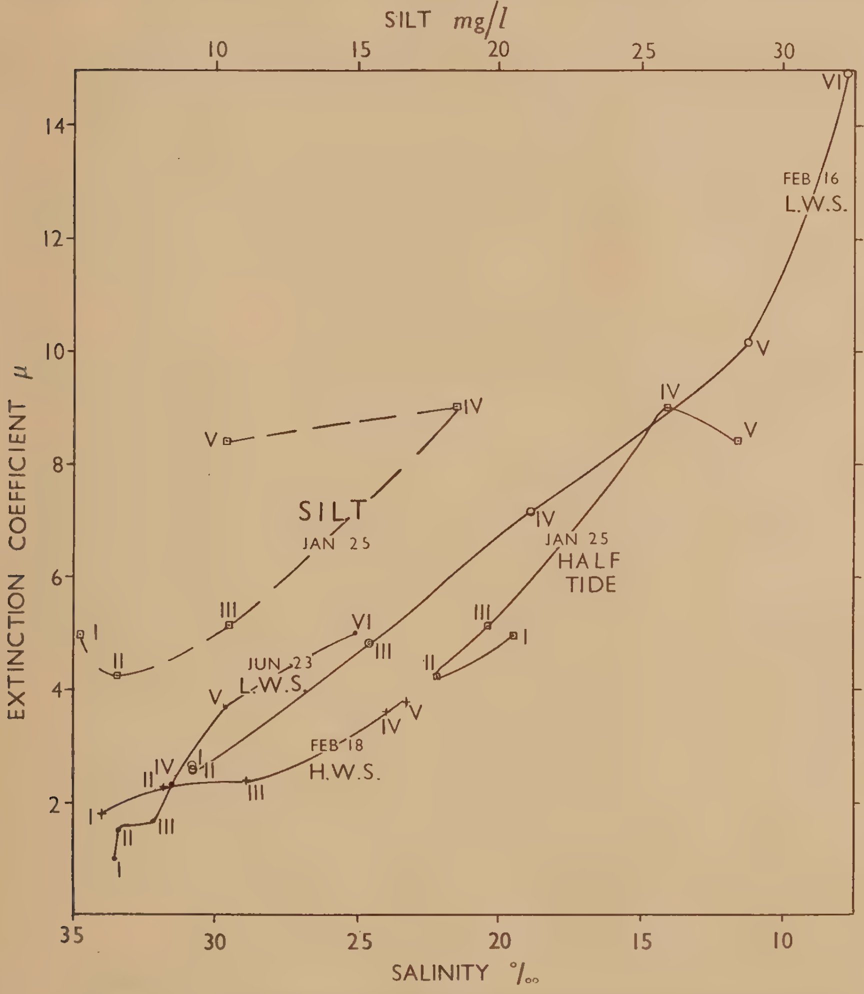


Fig. 2. Relation between extinction coefficient for green light (500 mμ.) and salinity, and also silt content on January 25 (pecked line). For key to positions of observations, see Fig. 3.

bringing with it a heavy load of silt. In February the surface waters of the estuary became so turbid that at low water at Neal Point with a salinity of 7·8 °/oo the intensity of red and blue light entering the water was cut down to one-thousandth within 0·6 and 0·4 m. respectively ($\mu = 12{\cdot}2$ and $16{\cdot}5$). Even

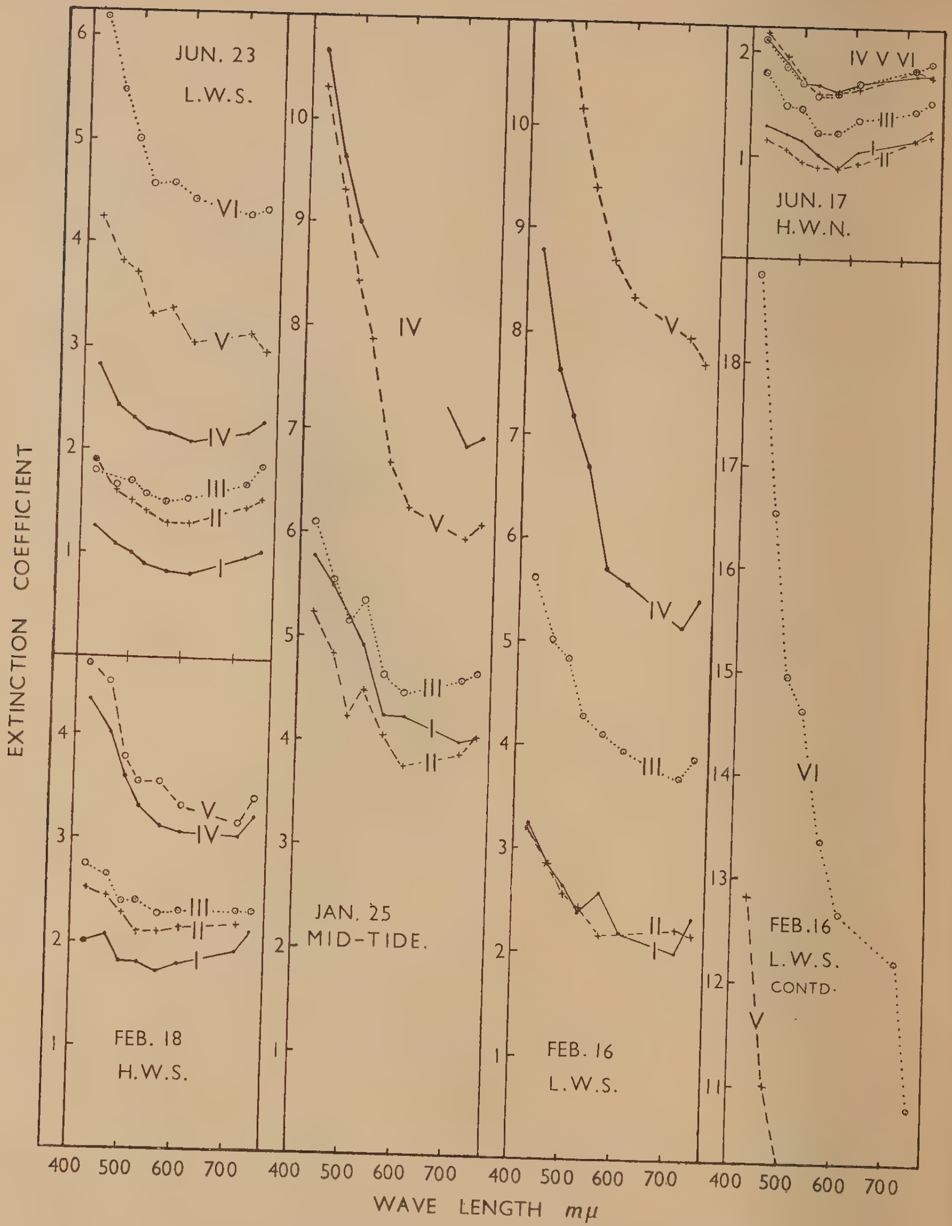


Fig. 3. Extinction coefficients in Plymouth Sound and Hamoaze.

I	——•——	Breakwater No. 1 Buoy.	IV	——•——	Hamoaze No. 7 Buoy.
II	----+----	Drake's Island No. 1 Buoy.	V	----+----	Hamoaze No. 15 Buoy.
III	····○····	Hamoaze No. 1 Buoy.	VI	····○····	Neal Point Buoy.

H.W.S.=High-water springs. L.W.S.=Low-water springs. H.W.N.=High-water neaps.

The curves for February 16 in the third panel are continued in the fourth.

at the two surface stations in Plymouth Sound, the coefficient for blue light was 2·85. This compares with the value for daylight, 2·52, found at the surface in Gullmar Fjord under somewhat similar weather conditions by Pettersson (1935).

The June measurements were made during a very dry spell (see Part III). The little rain that fell must have been absorbed by the soil, so that the fresh water draining to the river would be the minimum flow and composed of clear spring water and seepage from the moors. In consequence in June even at low water at Neal Point Buoy the surface salinity was no less than 25·1 $^{\circ}/_{\circ\circ}$, and the extinction coefficients were similar to those at high water in February. The February and June results probably represent the extremes of conditions likely to be encountered in the estuary.

Relative Extinction of Different Wave-Lengths

Visible light of shortest wave-length is transmitted by the violet S 43 filter, but within this wave-band the sensitivity of the eye and the composition of light in air are changing rapidly. Measurements made with that filter are therefore liable to considerable error. We have accordingly preferred to arrange our February and June results in order of increasing absorption of blue light (filter S 47). These have been divided into three groups having $\mu_{470} = 1–2{\cdot}1$, 2·4–2·9 and 3·8–16·5. The ratio of the extinction coefficient for each spectral filter relative to that for S 47 has been calculated for every sample. In each group the mean value for the ratio μ_λ/μ_{470} and the standard error when this is of interest have been computed (Table III). It will be seen that for light having μ_{470} greater than unity, light in the spectral region 400–570 mμ. (violet to orange) is always extinguished in the same proportions, viz. 1·11, 1·00, 0·92 and 0·86 at about 430, 470, 500 and 530 mμ. respectively. This is so no matter what the absolute magnitude of the coefficient may be, provided that it exceeds unity. For red light longer than 600 mμ., the more turbid the water the less is the extinction coefficient relative to that for blue (or for that matter green). The greater the wave-length within the visible spectrum the greater this difference becomes. For the group having $\mu_{470} = 1–2{\cdot}1$, the figures

Table III

	Mean ratios of μ_λ/μ_{470} for values of μ_{470} between			
Filter	1·0 and 2·1	2·4 and 2·9	3·8 and 16·5	Entire series
S 43	1·110	1·097	1·112	1·107
S 47	1·000	1·000	1·000	1·000
S 50	0·928	0·924	0·917	0·923
S 53	0·861	0·874	0·847	0·856
S 57	0·821 ± 0·015	0·854 ± 0·025	0·805 ± 0·015	0·823
S 61	0·860 ± 0·018	0·829 ± 0·024	0·766 ± 0·010	0·812
S 72	0·962 ± 0·019	0·830 ± 0·037	0·739 ± 0·016	0·855
S 75	1·010 ± 0·020	0·881 ± 0·043	0·742 ± 0·018	0·889

for the S 72 and S 75 filters may be in some error due to the uncertain distilled water correction. This source of error will be negligible in the other two groups and it does not apply to filter S 61.

Suspended particles affect the extinction of visible light in air and in water in the same way, favouring the transmission of red and yellow rather than blue and green. In marked contrast to pure clear air, pure water itself absorbs light in the extreme visible red and in the infra-red, so that such light is practically completely absorbed within 1 or 2 m., no matter what the turbidity may be (Poole & Atkins, 1937). In water, therefore, the region of optimum transmission will result from two opposing factors—absorption by suspended matter cutting out the blue and green and absorption by the molecules of water and dissolved salts cutting out the infra-red and often much of the visible red. Unlike foggy air, turbid water is unlikely ever to show an optimum transmission in the infra-red.

DEPTH AT WHICH SURFACE LIGHT IS REDUCED TO 1 %

The depths in metres (d_1) at which the intensity of light of given wave-length was cut down to one-hundredth of that incident on the surface are set out in Table IV in which the following assumptions are implicit:

(1) That the loss of light at the surface is 15 % of that incident there. Powell & Clarke (1936) have discussed in detail the various surface losses.

(2) That the water down to the depth given was uniform with that sampled at 0·3 m. (see p. 514).

(3) That the vertical depth is a sufficient measure of the effective path of the downward penetrating light. The arguments advanced by Atkins & Poole (1933, p. 140) for open sea water below 10 m. are considered to apply at a much lesser depth when scattering, as here, is so much greater.

The equation, $\mu = 4{\cdot}44/d_1$, may be used to recalculate from Table IV the extinction coefficients which have been plotted in Fig. 3. Also the depth, d_x metres, at which the intensity of light of given wave-length is reduced to x % of that incident on the surface may be found from the relation.

$$d_x = d_1\,(1 - 0{\cdot}518 \log_{10} x).$$

PERCENTAGE ENERGY COMPOSITION OF TRANSMITTED LIGHT

Abbot (see *Seventh Internat. Congress of Photography*, 1929) has measured the relative spectral energy composition of mean noon sunlight. If we take the relative energy figures appropriate to each of our filters, we can calculate the spectral energy composition of the light transmitted to any depth. Owing to the much greater transmission of light at about 720 than at 500 mμ. in very turbid water, it is not practical to express our results as did Poole & Atkins (1937, fig. 2). In Fig. 4 we show the spectral energy composition of mean noon sunlight reaching 1 m. at the more transparent stations relative to the energy at 500 mμ. in air as 100 %. For the more turbid stations, logarithmic

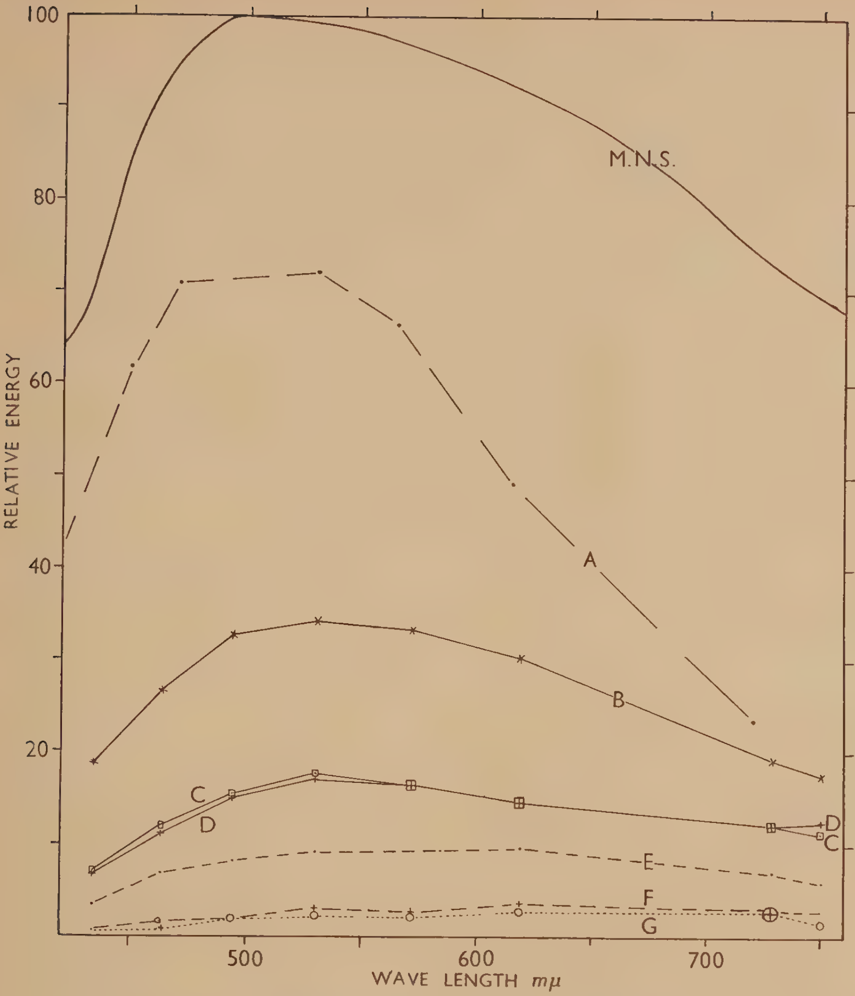


Fig. 4. Relative energy of mean noon sunlight at various wave-lengths transmitted to one metre. Allowance has been made for 15 % surface loss.

Key to Figs. 4 and 5.

June positions, high water: ————— February positions, high water: · · · · · · · · · · · ·
June positions, low water: — — — — — — February positions, low water: —···—···—

Curve *M.N.S.*	Mean noon sunlight in air (Abbot).
A	Photo-electric measurements by Poole & Atkins (1937), half mile east of Eddystone September 21 1936.
B	Drake's Island, No. 1 Buoy, high water June 17 1937.
C	Hamoaze, No. 15 Buoy, high water June 17.
D	Neal Point Buoy, high water June 17.
E	Hamoaze, No. 7 Buoy, low water June 23.
F	Hamoaze, No. 15 Buoy, low water June 23.
G	Hamoaze, No. 15 Buoy, high water February 18.
H	Neal Point Buoy, low water June 23.
K	Hamoaze, No. 7 Buoy, low water February 16.
L	Hamoaze, No. 15 Buoy, low water February 16.
M	Neal Point Buoy, low water February 16.

plotting is necessary (Fig. 5), and some curves are included in both figures to facilitate comparison. They show clearly how little of the incident spectral energy under estuarine conditions reaches even to 1 m. and also the extent to which red light (> 600 mμ.) is preferentially transmitted.

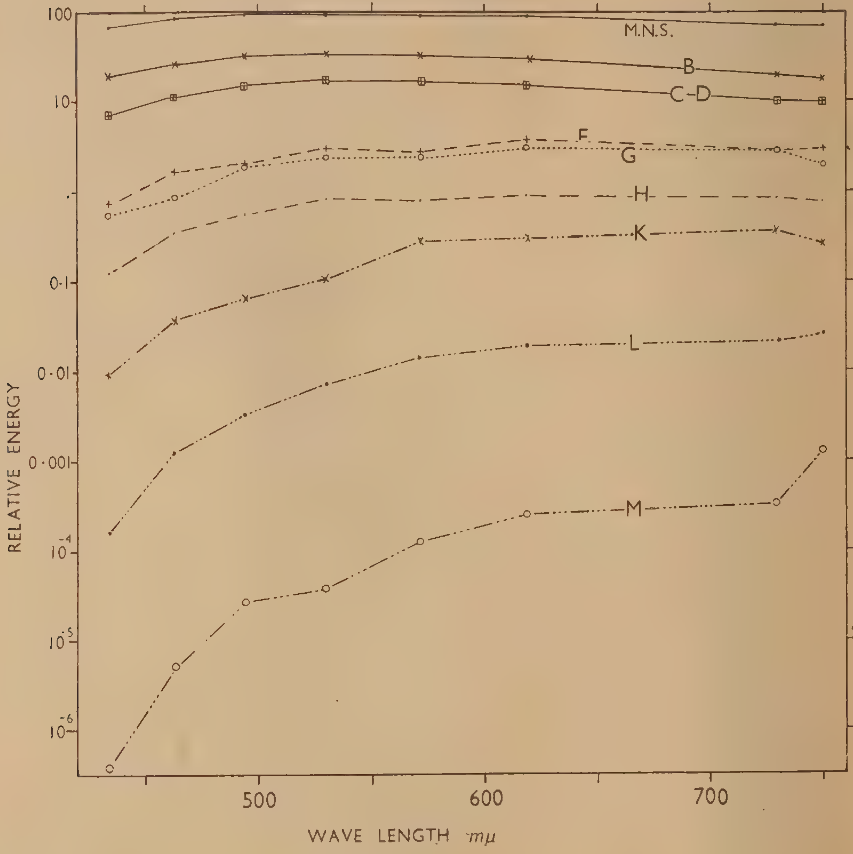


Fig. 5. Legend as for Fig. 4 except that relative energy is plotted on a logarithmic scale in order to include waters having high extinction coefficients.

If the extinction coefficients determined at Hamoaze No. 15 Mooring Buoy in February and in June are respectively plotted against salinity (as in Fig. 2), two curves are obtained which may be used to derive, from salinity records made on other occasions, extinction coefficients and the light intensities at 1 m. plotted in Fig. 6. It must be stressed very emphatically that this graph is intended to convey only a general picture of conditions in the

Hamoaze in the spring of 1937, when extensive ecological investigations were in progress, and not to represent exact results.

Preliminary experiments by H. Pettersson, Höglund & Landberg (1934) suggest that the compensation intensity at which photosynthesis just balances respiration by diatoms lies in the neighbourhood of 400 lux. The depths at which light energy incident on the surface is reduced to this value is therefore a rough measure of the compensation depth. The accurate calculation of this depth is very tedious, but a fair approximation may be made by taking the extinction coefficient for orange-red light (S 61 filter) as representing that of all the light transmitted by the turbid water found in our estuary. The figures for this filter in Table IV will then be a very rough measure of the compensation depth when the illumination in air is 40 kilolux. Such an illumination approximates to that of a bright sunny day at the end of February or of an overcast day in summer (Atkins & Poole, 1936). On a cloudless summer day an intensity of 120 kilolux in air may be exceeded, and the compensation depth would lie about 25 % deeper.

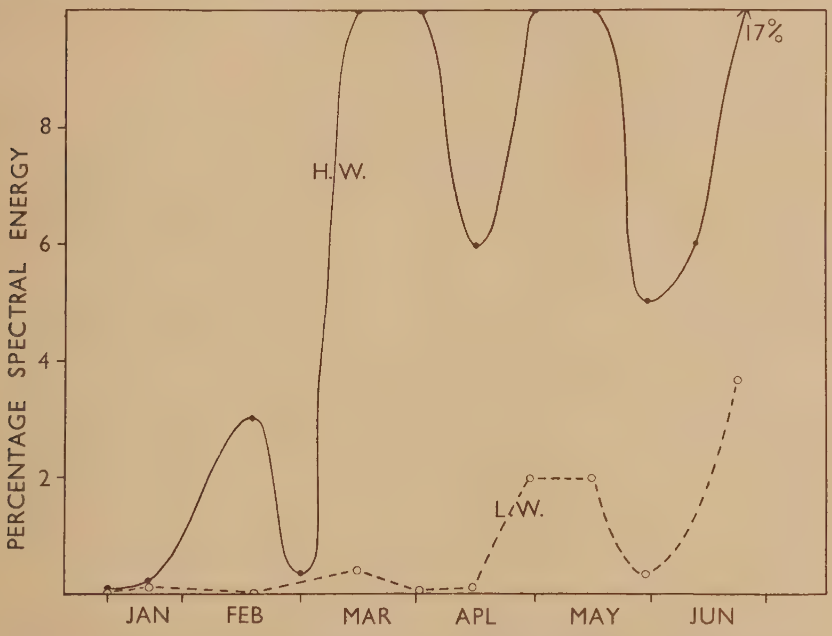


Fig. 6. Percentage spectral energy between 410 and 760 mμ. transmitted to one metre at high and at low water near Mooring Buoy No. 15 in Hamoaze, January to June 1937. Based on salinity records (see text).

TABLE IV. DEPTH IN METRES AT WHICH INTENSITY OF LIGHT IS REDUCED TO 1 % OF THAT INCIDENT ON THE SURFACE
Assuming 15 % Surface Loss; $\mu d_1 = 4{\cdot}444$

Centre of gravity of filter mμ.	Breakwater No. 1 Buoy	Drake's Island No. 1 Buoy	Hamoaze			Neal Point Buoy
			No. 1 Buoy	No. 7 Buoy	No. 15 Buoy	
February 18 1937. Spring tide. High water						
434	2·20	1·76	1·62	1·02	0·95	...
463	2·06	1·81	1·67	1·09	0·98	...
494	2·45	1·95	1·85	1·23	1·17	...
530	2·45	2·12	1·85	1·34	1·25	...
572	2·58	2·12	1·95	1·42	1·25	...
619	2·48	2·06	1·93	1·45	1·34	...
729	2·31	2·02	1·92	1·46	1·41	...
750	2·11	1·79	1·91	1·38	1·31	...
February 16 1937. Spring tide. Low water						
434	1·37	1·39	0·79	0·51	0·35	0·24
463	1·56	1·55	0·89	0·58	0·40	0·27
494	1·68	1·73	0·92	0·62	0·43	0·30
530	1·86	1·82	1·04	0·67	0·47	0·30
572	1·72	2·05	1·08	0·78	0·51	0·33
619	2·02	2·03	1·12	0·80	0·53	0·35
729	2·22	1·99	1·20	0·86	0·56	0·36
750	1·90	2·03	1·14	0·82	0·58	0·41
June 17 1937. Neap tide. High water						
434	3·44	3·83	2·48	2·09	2·02	2·10
463	3·64	4·15	3·00	2·34	2·27	2·38
494	3·86	4·68	3·04	2·60	2·58	2·60
530	4·40	4·93	3·61	2·64	2·76	2·81
572	5·00	4·93	3·58	2·76	2·77	2·77
619	4·23	4·73	3·28	2·61	2·69	2·62
729	3·76	3·77	3·08	2·48	2·41	2·40
750	3·52	3·63	2·90	2·48	2·50	2·33
June 23 1937. Spring tide. Low water						
434	3·52	2·36	2·50	1·57	1·05	0·72
463	4·11	2·78	2·68	1·83	1·16	0·81
494	4·40	2·94	2·63	1·92	1·20	0·89
530	5·05	3·17	2·84	2·02	1·34	0·96
572	5·42	3·47	2·97	2·06	1·32	0·96
619	5·62	3·47	2·92	2·14	1·46	1·00
729	4·67	3·08	2·66	2·04	1·42	1·03
750	4·35	2·90	2·40	1·95	1·50	1·02

ZONATION OF ALGAE ON BUOYS

The flora on the mooring buoys in Plymouth Sound and the Hamoaze may be divided into three zones with clearly marked boundaries.* The depths of these zones vary and may be correlated with differences in illumination.

The daylight factors (percentages of vertical white light having the spectral composition of mean noon sunlight) have been worked out for each of the zonal boundaries (Table V); the zones and their daylight factors vary little within Plymouth Sound, mean figures for which are given. The similarity of the daylight factors in the Sound and at No. 7 Buoy in the Hamoaze on three occasions—at high and low water in June and at high water in February—shows that variations in illumination are adequate to account for the zonation found. The plants in Zone I require a surprisingly high proportion of the incident light. Even at the top of Zone III, a daylight factor as high as 67 % can occur.

---

* Paper in preparation by A. M.

TABLE V. DAYLIGHT FACTORS AT BOUNDARIES OF ALGAL ZONES ON BUOYS

No correction for surface loss

	Zone I		Zone II	
	Plymouth Sound	Hamoaze No. 7 Buoy	Plymouth Sound	Hamoaze No. 7 Buoy
Depth of bottom of zone, m. ...	0·18	0·097	0·356	0·223
Daylight factor, %:				
June 17 (high water)	83·6	84·6	68·5	67·4
June 23 (low water)	80·8	80·6	65·5	60·4
February 18 (high water)	69·0	72·2	47·2	47·3
February 16 (low water)	64·6	54·6	42·3	25·3

The algae composing Zone III were found in a flourishing condition right to the bottom of all the buoys examined. The daylight factors at the bottom of the two deepest buoys are set out in Table VI. Account has been taken neither of surface losses nor of shading by the buoys themselves. Some of the adult algae no doubt float upwards into water receiving more light than shown, but in their young stages they must be able to grow in water having a daylight factor always less than 1·5 % and often less than 0·5 %.

TABLE VI. DAYLIGHT FACTORS AT BOTTOM OF TWO BUOYS (WITHIN ZONE III)

	Mallard Buoy (Plymouth Sound)			Hamoaze No. 7 Buoy		
Date and state of tide	Depth of bottom of buoy m.	Daylight factor %	Wave-length of maximum transmission mμ.	Depth of bottom of buoy m.	Daylight factor %	Wave-length of maximum transmission mμ.
June 17 (high water)	2·19	10·16	570	2·47	1·35	580
June 23 (low water)	2·19	7·59	580	2·47	0·42	630
February 18 (high water)	2·19	1·16	580	2·47	0·035	650
February 16 (low water)	2·19	0·59	650	2·47	0·000093	720

SUBMARINE DAYLIGHT IN THE NORTH SEA

The numerous determinations of turbidity made in the southern North Sea by Kalle (1937) in January 1935 and February 1936, using the Pulfrich photometer with the red S 72 filter, may be used to derive the extinction coefficient for red light for comparison with results elsewhere. He reported his results as "*K*-values" which are a measure of the extinction as measured in a 0·25 m. tube. When the extinction coefficient as measured is defined by equation (3), it may be shown that $\mu_M = \frac{9{\cdot}2\,K}{1000}$. From equation (4) the true extinction coefficient for the sea water

$$\mu_{SW} = \frac{9{\cdot}2\,K}{1000} + \mu_{DW},$$

and the depth in metres at which the light is reduced to 1 % of that incident on the surface (as in Table IV)

$$d = \frac{4440}{9{\cdot}2\,K + 1000\,\mu_{DW}},$$

where K is Kalle's measure of turbidity. These expressions may not be accurate for values of K less than 100, since any error in the correction factor, μ_{DW}, becomes large and a surface sample only will be inadequate to characterize all the water concerned in the absorption of light. Moreover, for such waters a 0·25 m. absorption tube may be too short.

Assuming, as in our work, that $\mu_{DW} = 0{\cdot}47$, the true extinction coefficients have been calculated for some of Kalle's more turbid stations (Table VII). These appear to be of two types, one being practically isohaline and showing greater turbidity and light extinction coefficient at the bottom than at the surface, the second having much lower salinity and higher extinction coefficient at the surface and resembling our own conditions in Hamoaze. Water of the

TABLE VII. A COMPARISON BETWEEN EXTINCTION COEFFICIENTS FOR RED LIGHT (S 72 SPECTRAL FILTER) IN THE NORTH SEA (DERIVED FROM KALLE 1937) AND IN THE HAMOAZE

Station	Date	Position	Depth m.	Salinity ‰	Extinction coefficient μ_{SW}
		Group 1			
12d	i. 35	52° 53′ N 2° 27′ E	0	34·71	3·5
			34	34·71	5·0
13	i. 35	52° 41·5′ N 2° 17·5′ E	0	34·66	3·6
			48	34·60	12·9
16	i. 35	52° 16·7′ N 1° 50′ E	0	34·45	7·8
			28	34·49	12·9
17	i. 35	52° 10·1′ N 2° 12′ E	0	35·16	2·4
			43	35·01	6·3
27	i. 35	51° 30·8′ N 1° 26·1′ E	0	35·05	3·2
			14	35·01	6·2
		Group 2			
60	i. 35	Off Rhine-Meuse Delta	0	25·63	4·3
			22	33·86	1·5
70	ii. 36	Channel N. of Sylt off	0	30·01	7·9
71	ii. 36	Schleswig	0	28·35	10·0
84	ii. 36	Off Mouth of Elbe	0	23·55	7·8
85	ii. 36	,,	0	15·50	12·0
86	ii. 36	,,	0	16·04	12·0
		Hamoaze, No. 15 Buoy:			
—	ii. 37	High water	0·3	23·3	3·1
—	ii. 37	Low water	0·3	11·2	8·0
—	ii. 37	Neal Point, low water	0·3	7·7	12·2

first type occurred off the East Anglian coast, and most of the suspended matter must have been stirred up from the bottom by tidal or storm action. Extinction coefficients calculated only from surface data will be too low. Part of this region of high absorption is associated with the north-west Southern Bight Eddy which Kalle discovered as a result of these cruises.

Water of the second type was found at the mouths of the Elbe and of the Rhine-Meuse delta. As in the Hamoaze, also in February, the suspended matter had no doubt been brought down by flood water from the rivers. Since these are much larger than those feeding the Hamoaze, the region of low salinity and high absorption extended farther to sea. In the North Sea off East Anglia and in the sea off these continental river mouths the light absorption may be as high as in the Hamoaze under extreme conditions (Table VII). The special distribution of plants in estuaries is usually attributed primarily to reduced salinity. Whilst this is often true, there may be cases where the distribution is the result not of reduced salinity but of increased light absorption resulting from the associated silt. A study of the flora of buoys situated off the East Anglian coast along the lines followed by one of us (A. M.) in the Hamoaze might go far towards a solution of the problem.

Some Biological Indications

From Table IV it will be seen that even under optimum conditions light is always reduced to 1% or less within 5 m. at Drake's Island No. 1 Buoy and within 3 or 4 m. further up the Hamoaze. In Table VIII a comparison is made with conditions in other waters determined photo-electrically by various workers. Whereas the same intensity of blue light (450 or 470 mμ.) was found

Table VIII. Depth in metres at which light of various wave-lengths is reduced to 1% (as in Table IV)

Station	Date	Wave-length mμ.							
		400	450	470	530	570	600+	675+	700+
Coasts of Iceland*	May 1934	...	...	2·0– 12·0	2·4– 19·3	...	...	...	...
Plymouth Breakwater†	Oct. 1932	...	6·3	...	10·7	...	4·6	3·0	...
Puget Sound, Pillar Point‡	June 1934	...	8·7	9·7	12·2	13·3	8·8	...	...
Puget Sound, Pillar Point	Jan. 1934	...	21·5	26	30	26	13·0	...	...
Puget Sound, Hood Canal‡	Apl. 1934	...	6·6	9·4	17·7	14·5	8·2	...	...
Puget Sound, Hood Canal	Mar. 1934	...	18·9	21	29	23	12·7	...	...
English Channel, Eddystone†	Sept. 1936	14·8	34	38	41	31	10·5	...	3·6
Pacific Ocean, 47° 26′ N., 126° 26′ W.§	...	...	63	62	59	43	14·7	9·1	...
Sargasso Sea‖	...	100	148	...	85	...	17	...	...

* Measurements with Pulfrich photometer by Steemann Nielsen (1935). Results at 490 mμ. entered as 470 mμ.

† Photo-electric measurements by Poole & Atkins (1937).

‡ Photo-electric measurements by Williams & Utterback (1935). Records at 460, 480 and 565 mμ. entered as 450, 470 and 570 mμ. respectively.

§ Photo-electric measurements by Utterback & Jorgensen (1934).

‖ Photo-electric measurements by Clarke (1936). Read from a graph of μ_v.

at 0·27 m. at Neal Point Buoy under the worst conditions and at 148 m. in the Sargasso Sea (ratio 1 : 550), the corresponding figures for red light were 0·36 and 17 m. (ratio 1 : 48).

Not only will the reduced light intensity compress the zonation of plants in estuarine waters but the season of active growth should be shorter than in the open sea. Moreover, both these effects should become more marked in an up-river direction, and species dwelling near the level of low water should be more affected than those nearer high-water mark.

We are much indebted to Dr W. R. G. Atkins and Dr H. H. Poole for their helpful advice.

SUMMARY

The Zeiss Pulfrich photometer, with its eight spectral filters covering narrow spectral bands within the visible spectrum, has been used to investigate the penetration of light into an estuary under winter and summer conditions.

Throughout the visible spectrum, extinction coefficients in Hamoaze are always higher, in winter often very much higher, than in the English Channel. In marked contrast to the open sea, red light penetrates as well or better than green, and blue is cut down most rapidly. Highest and lowest values of μ found at two estuarine stations were:

		Hamoaze No. 1 Buoy		Neal Point Buoy	
Colour		Lowest	Highest	Lowest	Highest
Blue	440–480 mμ.	1·48	5·01	1·87	16·5
Green	515–550 mμ.	1·23	4·28	1·58	14·6
Red	610–640 mμ.	1·35	3·94	1·69	12·7
Dark red	710–760 mμ.	1·44	3·69	1·85	12·1

The intensity of incident daylight in the Hamoaze appears always to be reduced to 1 % within 4 m., often in less than 2 m. and at low water when the rivers are in spate in less than 0·5 m.

For water having an extinction coefficient for blue light (470 mμ.) greater than unity, the light within the spectral range 400–570 mμ. is always extinguished in the same proportions ($\mu_\lambda/\mu_{470} = 1·11$, 1·00, 0·92 and 0·86 at about 430, 470, 500 and 530 mμ. respectively).

For red light longer than 600 mμ., the more turbid the water the less is the extinction coefficient relative to blue (or for that matter green). The greater the wave-length within the visible spectrum the greater the difference becomes.

Zonation of algae on buoys may be correlated with variations in illumination.

Measurements of turbidity in the North Sea by Kalle have been recalculated to give the extinction coefficient for red light. Off the East Anglian coast and off the mouths of the Elbe and the Rhine-Meuse delta, very turbid waters showing values of μ_{720} as high as 12·9 were encountered.

REFERENCES

ASCHKINASS, E. VON, 1895. Ueber das Absorptionspectrum des flüssigen Wassers und über die Durchlässigkeit der Augenmedien für rothe und ultrarothe Strahlen. *Wied. Annal. Physik. Chemie*, Vol. 55, pp. 401–31; cited by Sawyer (1931).

ATKINS, W. R. G. & POOLE, H. H., 1933. The photo-electric measurement of the penetration of light of various wave-lengths into the sea and the physiological bearing of the results. *Phil. Trans. Roy. Soc.*, Ser. B, Vol. 222, pp. 129–64.

ATKINS, W. R. G. & POOLE, H. H., 1936. The photo-electric measurement of the diurnal and seasonal variations in daylight and a globe integrating photometer. *Phil. Trans. Roy. Soc.*, Ser. A, Vol. 235, pp. 245–72.

CLARKE, G. L., 1936. Light penetration in the western North Atlantic and its application to biological problems. *Rapp. Proc.-verb. Cons. Int. Expl. Mer*, Vol. CI, 2ème Partie, no. 3, pp. 1–14.

DAWSON, L. H. & HULBURT, E. O., 1934. The Absorption of Ultraviolet and Visible Light by Water. *Journ. Opt. Soc. Amer.*, Vol. 24, 175–7.

HARTLEY, P. H. T. & SPOONER, G. M. 1938. The Ecology of the Tamar Estuary. I. Introduction. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 501–8.

KALLE, K., 1931, 1935. Meereskundliche chemische Untersuchungen mit Hilfe des Zeißschen Pulfrich-Photometers. I. Mitt. Apparatur. V. Mitt. Die Bestimmung des Gesamt-Phosphorgehaltes (lebende Substanz) und Trübungsmessungen. *Ann. d. Hydr.*, Jahrg. LIX, pp. 313–17 and Jahrg. LXIII, pp. 195–204.

—— 1937. Nährstoff-Untersuchungen als hydrographisches Hilfsmittel zur Unterscheidung von Wasserkörpern. *Ann. d. Hydr.*, Jahrg. LXV, pp. 1–18.

LANGE, B. & SCHUSTERIUS, C., 1932. Die Absorption des Wassers im sichtbaren Spektralgebiet. *Zeits. physikal. Chem.*, Abt. A, Bd. 159, pp. 303–5; Berichtigung, ibid., Bd. 160, Heft 6.

MILNE, A., 1938*a*. The ecology of the Tamar Estuary. III. Salinity and temperature conditions in the lower estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 529–42.

NIELSEN, E. STEEMANN, 1935. The production of phytoplankton at the Faroe Isles, Iceland, East Greenland and in waters around. *Medd. Komm. Danmarks Fisk. og Havundersøgelser*, Ser. Plankton, Bd. III, pp. 1–93.

PETTERSSON, H., 1935. Submarine daylight and the transparency of sea water. *Journ. Cons. Int. Expl. Mer*, Vol. X, pp. 48–65.

PETTERSSON, H., HÖGLUND, H. & LANDBERG, S., 1934. Submarine daylight and the photosynthesis of phyto-plankton. *Göteborgs kungl. Vetenskaps- och Vitterhets-Samhälles Handlingar.* Femte Följden, Ser. B, Bd. 4, No. 5, pp. 1–17.

POOLE, H. H. & ATKINS, W. R. G., 1926. On the penetration of light into sea water. *Journ. Mar. Biol. Assoc.*, Vol. XIV, pp. 177–98.

—— —— 1937. The penetration into the sea of light of various wave-lengths as measured by emission or rectifier photo-electric cells. *Proc. Roy. Soc.*, Ser. B, Vol. 123, pp. 151–65.

POWELL, W. M. & CLARKE, G. L., 1936. The reflection and absorption of daylight at the surface of the ocean. *Journ. Opt. Soc. Amer.*, Vol. 26, pp. 1–23.

SAWYER, W. R., 1931. The spectral absorption of light by pure water and Bay of Fundy water. *Contrib. Canadian Biol. and Fish.*, N.S., Vol. VII, pp. 73–89.

UTTERBACK, C. L. & JORGENSEN, W., 1934. Absorption of Daylight in the North Pacific Ocean. *Journ. Cons. Int. Expl. Mer*, Vol. IX, pp. 197–209.

WILLIAMS, E. A. & UTTERBACK, C. L., 1935. Seasonal changes in components of submarine daylight. *Journ. Opt. Soc. Amer.*, Vol. 25, pp. 1–10.

THE ECOLOGY OF THE TAMAR ESTUARY

III. SALINITY AND TEMPERATURE CONDITIONS IN THE LOWER ESTUARY

By A. Milne, M.A., B.Sc.

Natural History Department, University of Aberdeen

(Text-figs. 1–5)

CONTENTS

	PAGE
Salinity Conditions in a Cross-section of the Estuary	529
Seasonal Surface Variations in Salinity	534
Rainfall and Salinity	537
Other Surface and Bottom Records of Salinity	538
Temperature of the Surface Waters	540
Hydrogen-Ion Concentration	541
Summary	542
References	542

In the Tees Survey (Alexander, Southgate & Bassindale, 1935) the general salinity conditions of the Tees Estuary have been clearly described, and it was suggested that conditions in the Tamar might be somewhat similar. Observations during 1936–37 confirm this similarity. Here, therefore, it is only necessary to discuss those data which will give some idea of the actual salinity fluctuations (rate of change as well as magnitude) affecting the fauna and flora of the section of the Tamar Estuary now considered in these papers.

The Tees Survey gives maximum, minimum, and average salinities, but such data are not the only aspects to be considered from the point of view of salinity effects on organisms, for it is well known that some aquatic animals can be acclimatized to almost any salinity from above that of sea water down to fresh water, provided that the change is brought about gradually. The actual range of salinity may not be so important as rate of change.

SALINITY CONDITIONS IN A CROSS-SECTION OF THE ESTUARY

In the Tees Estuary (1935, p. 76) "The salinity variation to which an organism is subjected depends, therefore, on the position in the intertidal area at which the species normally lives. A mean value has been taken as the difference between salinity at the surface at low water under normal winter conditions and at a depth of one fathom at high water under normal summer conditions. Organisms living near high-water mark suffer a smaller, and those living near low-water mark a greater variation than this mean value." To give a more complete picture of events in the Tamar Estuary, two investigations of salinity conditions at various depths in a cross-section of the river at a representative estuarine position were made on a rising tide and on a falling tide. The rainfall was slightly above normal in the former and normal in the latter (see rainfall in Fig. 3). The first of these sets of observations was carried out on May 24 1937, when the predicted height of the tide was 4·35 m., and the second on June 3, when it was 3·76 m. Normally tidal heights range from about 3 to 5 m. above chart datum.

For the positions mentioned in this paper the map reproduced in Part I of this series (Hartley & Spooner, 1938) should be consulted.

That the area under consideration in this ecological study is a natural compartment or division of the estuary is emphasized by the following extract from Percival (1929): "It would appear that the main body of incoming sea water does not pass Cargreen. A considerable portion goes into the Lynher and Tavy and covers the mud-flats on each side between Saltash and Neille* Point. A further large quantity is held over the flats between Neille Point and Hole's Hole." Our observations were made about midway between Saltash Bridge and Neal Point (7·7 km. from mouth of estuary), a position chosen because it lies near the middle of the area under consideration and in a fairly straight stretch of the river. Collections were taken (at hourly intervals) at nine points, marked by buoys, in the cross-section—one in mid-river and four in each of the intertidal areas from high-water mark to low-water mark. Sampling was done by means of a reversing bottle at $\frac{1}{2}$ or 1 m. intervals from the bottom to the surface. Salinities were determined with immersion hydrometers and temperature corrections made. Depth was plotted against time for each of the nine stations and, upon these, isohaline curves were superimposed by means of salinity-depth curves; finally isohalines on a cross-section of the river at intervals of 1 hr. were drawn as in Fig. 1.

It is seen that on a rising tide the Cornish margin is a little less saline than the Devon, and on a falling tide the reverse is true. This lag may be explained by the contour of the river and does not alter the general fact that when the tide is rising there is an "up-bulging" of the more saline layers from the bottom in the middle; and when it is falling there is a "down-bulging" of the less saline or fresh layers of the river. This bulging is produced by friction at the edges, where the water is shallow, tending to retard water movement in that region as compared with the middle or deeper part. It must be remembered that the bulging is exaggerated in Fig. 1 owing to the differences between the horizontal and vertical scales.

Owing to this bulging the surface water tends to be a little more saline in mid-river than at the edges at high water, and *vice versa* at low water. Fig. 1 shows that, in this region of the estuary, salinity stratification in mid-river at low water is much more pronounced than at high water, the range being greater though the salinity is less. The action of the river interferes slightly with the usual tidal oscillation.

It would be interesting to know the magnitude, range and duration of

---

* In these reports, following recent Ordnance maps, the spelling "Neal" is adopted.

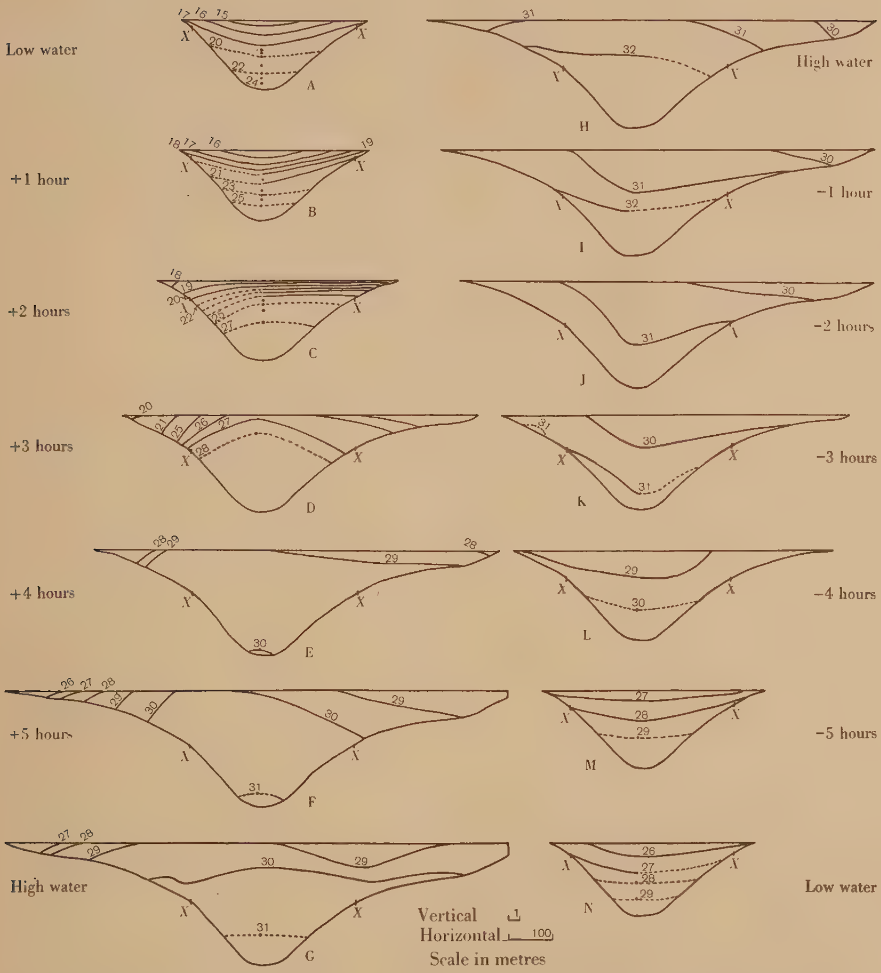


Fig. 1. Isohalines on a cross-section of the Tamar Estuary (midway between Saltash and Neal Point). *A–G* on May 24, *H–N* on June 3 1937. *X* is low-water mark of equinoctial spring tides. Cornwall to the left, Devon to the right of each section. Dotted lines indicate insufficient data—sometimes only one record at the level in question. Single dots between isohaline curves indicate intermediate salinities, e.g. in Section A two dots between isohalines 17 and 20 show the levels in mid-river at which salinities of 18 and 19°/₀₀ were obtained. The sections represent conditions at hourly intervals between high and low water.

incidence of salinities experienced by organisms at various points on the estuary bed over a period of several years. The work attached to such an investigation is not practicable, but some insight into the problem may be got by a study of data compiled from Fig. 1 (see Fig. 2 and Table I). The positions chosen were (*a*) bottom mid-river, (*b*) mean high water of spring tides, (*c*) mid-tide mark, and (*d*) mean low water of spring tides. The fluctuation in the water layers above bottom mid-river need not be studied because this region is inhabited principally by plankton which moves with the currents and therefore stays in water of more or less suitable salinity. The only animals of importance in this region are fishes which can avoid low salinities by going deeper, and also the organisms living on the mid-river buoys (the latter are dealt with in Part IV of this series). Fig. 2 is drawn from data obtained on the Devon shore on May 24; the conditions on the Cornish bank were similar.

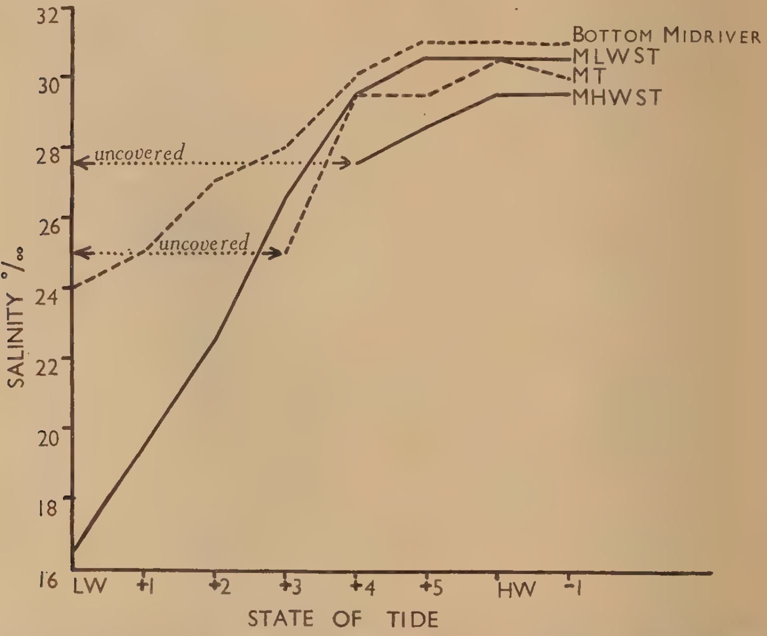


Fig. 2. Salinity fluctuation at different levels. May 24 1937. Midway between Saltash and Neal Point, Devon bank. The periods during which H.W.M. and M.T. mark are uncovered by the tide are indicated. M.L.W.S.T. is mean low-water (mark) of spring tides. M.H.W.S.T. is mean high-water (mark) of spring tides. M.T. is mid-tide mark. L.W. is low water; H.W. is high water. Numbers 1–5 represent hours.

In this section of the estuary, near high-water mark, organisms suffer least fluctuation, and those near low-water mark suffer most; while those at mid-tide mark experience a fluctuation intermediate between these two. That is, there is a fluctuation gradient decreasing from low-water mark to high-water mark. An organism at low-water mark experiences the greatest and least salinities possible in the intertidal area and indeed in the entire estuary bed; at high-water mark, while the fluctuation is very much less, it is important to note that it is also in the higher end of the salinity range. On proceeding from low-water mark to high-water mark the upper limit of the salinity range falls only very slightly, while the lower rises considerably. Thus the higher the level in the intertidal area at which an organism lives the more favourable the salinity conditions it will meet.

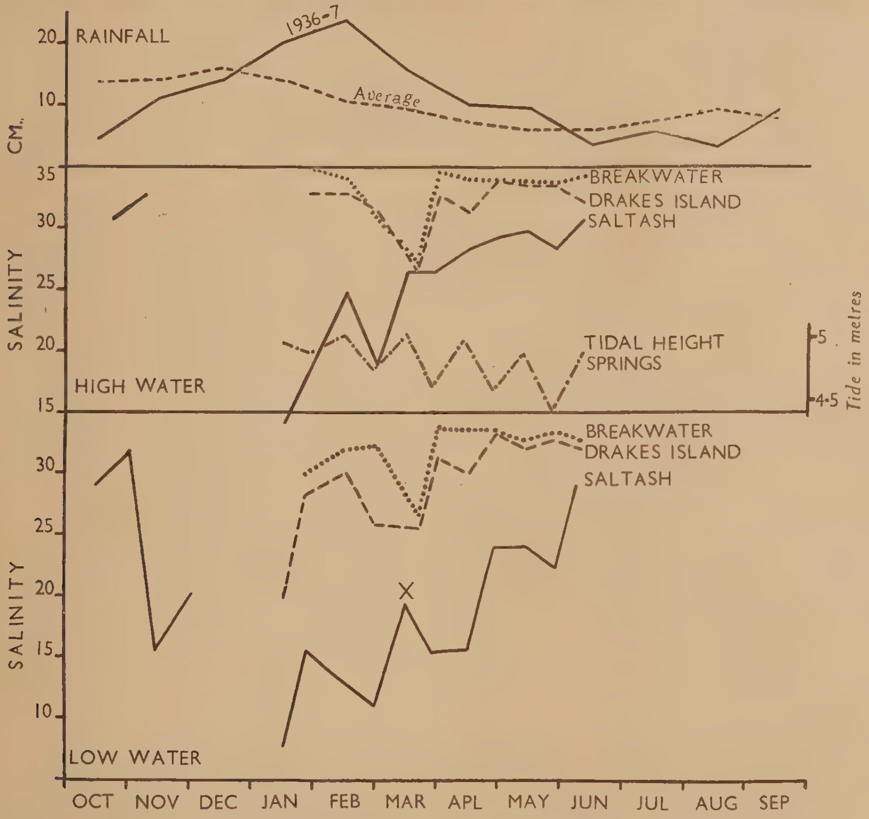


Fig. 3. Salinities for springs at high and low water—a continuous record from January to June 1937. Tidal height in metres. Total monthly rainfall for Tamar Valley Area (average of eight stations) 1936–7; and normal average monthly rainfall for Egloskerry (one of these stations). Point *X* is referred to in the text.

Another aspect of possible biological importance is the duration of the period of fluctuation. Near high-water mark, not only is the fluctuation smaller than at points lower in the intertidal area and higher in the salinity range, but organisms are subjected to fluctuation for a shorter time. Owing to stratification, the farther down one goes in the intertidal area the longer is the duration of incidence of the high salinity (cf. Figs. 1 and 2); this will be more evident in winter than in summer for stratification is more pronounced in rainy periods.

Fig. 2 shows that organisms at bottom mid-river and at mid-tide mark (in this section of the estuary) experience a salinity fluctuation similar in range. The salinity change at mid-tide mark, however, takes place at approximately twice the rate of the change at the bottom mid-river; therefore the former position would be more dangerous to organisms affected by rate of fluctuation.

At low-water mark the fluctuation was high—from 16 to 30°/₀₀ in about 4 hr.; this was followed by a high, relatively steady salinity (over 30°/₀₀) for 4 hr.; then as sudden a drop as the original rise in another 4 hr. The osmotic changes to which an organism would be subjected are thus considerable, i.e. *ca.* 10 atm. in 4 hr.

The data given in Fig. 2 are for a specific day—May 24 1937, but considering the height of the tide, the rainfall and other factors, they cannot be very far short of normal winter conditions. The series for June 3 (see Table I) must approximate to summer conditions. Fluctuation may be a little less than on June 3 during drought, but it will be appreciably greater than on May 24 during a winter spate. Some indication of the maximum and minimum salinities for the season in question may be gained from Fig. 3 and data given on pp. 538–9. The effect of these positional fluctuations on the horizontal up-river penetration of marine organisms will be discussed in a later paper.

Seasonal Surface Variations in Salinity

In an investigation of the fauna and flora of the mid-river buoys it was found necessary to have some idea of the surface salinities in mid-river. They were taken at a depth of 1 ft. (0·3 m.). At high and low water of spring tides samples were regularly taken at three positions in the estuary (Table II) and supplemented by open-sea observations taken at the same time. At spring tides the maximum and minimum salinities (river-flow and wind being normal) may be expected since it is at this time that the sea advances and recedes farthest in any estuary.

Saltash No. 15 Mooring Buoy (6 km. from mouth), and Drake's Island, No. 1 Mooring Buoy (– 2·5 km. from mouth), were taken always at exactly high and low water; Breakwater, No. 1 Mooring Buoy,* within 90 min. on either side of the tide on the few occasions on which the times of collection did not coincide

---

* Position outside the area covered by the map of the estuary: it is well out in Plymouth Sound, 2 km. due S. of the W. end of Drake's Island.

TABLE I. SALINITY °/₀₀ AT VARIOUS POINTS ON THE ESTUARY BED

At hourly intervals between High Water (H.W.) and Low Water (L.W.)

	Mean low-water mark of spring tides		Mid-tide mark		Mean high-water mark of spring tides			
State of tide	Devon bank	Cornish bank	Devon bank	Cornish bank	Devon bank	Cornish bank	Bottom mid-river	Date
L.W.	16–17	17–18	...	...	...	...	24	May 24 1937
+1	19–20	18–19	...	...	...	...	25	
+2	22–23	19–20	...	...	...	...	27	
+3	26–27	26–27	25	20–21	...	...	28	
+4	29–30	29–30	29–30	29	27–28	26	30	
+5	30–31	30–31	29–30	29–30	28–29	26–27	31	
H.W.	30–31	30–31	30–31	30	29–30	28–29	31	
−1	30–31	30–31	30	30	29–30	27–28	31	
H.W.	31–32	32	30–31	31–32	29–30	31	32·5	June 3 1937
−1	31–32	32	30–31	31–32	29–30	31–32	32	
−2	31	31–32	30–31	31–32	29–30	30	32	
−3	30–31	31	29–30	30–31	...	...	31·5	
−4	29–30	29–30	...	...	...	...	30	
−5	28–29	28	...	...	...	...	29·8	
L.W.	26–27	27	...	...	...	...	29·9	

TABLE II. HIGH- AND LOW-WATER SURFACE SALINITIES AND TEMPERATURES AT SPRING TIDES

Samples taken at 1 ft. (0·3 m.) below surface

		Breakwater No. 1 Mooring Buoy		Drake's Island No. 1 Mooring Buoy		Saltash No. 15 Mooring Buoy	
Date 1937	State of tide	Salinity °/₀₀	Temp. °C.	Salinity °/₀₀	Temp. °C.	Salinity °/₀₀	Temp. °C.
Jan. 16	H.W.	...	...	...	...	14·0	...
	L.W.	...	...	19·5	...	7·6	...
Jan. 29	H.W.	34·9	8·9	32·7	8·9	18·2	7·0
	L.W.	29·7	8·1	28·1	8·9	15·6	8·5
Feb. 15	H.W.	34·0	9·85	32·7	9·6	24·6	9·5
	L.W.	31·7	9·8	29·8	9·5	12·9	10·5
Mar. 1	H.W.	30·7	8·4	31·1	8·5	18·9	6·5
	L.W.	32·0	8·95	25·6	7·6	10·8	6·5
Mar. 19	H.W.	26·9	9·4	26·4	9·0	26·4	8·0
(Saltash, Mar. 16)	L.W.	26·6	9·0	25·3	9·1	19·3	7·25
Apr. 1	H.W.	34·5	9·2	32·5	8·4	26·4	7·0
(Saltash, Mar. 30)	L.W.	33·6	9·2	31·1	8·6	15·3	6·5
Apr. 14	H.W.	33·8	10·4	31·1	10·0	28·2	9·5
	L.W.	33·4	10·6	29·9	10·8	15·4	11·5
Apr. 29	H.W.	33·7	10·8	33·7	11·2	29·1	11·0
	L.W.	33·4	11·3	33·3	12·1	23·8	12·0
May 14	H.W.	33·6	11·1	33·4	12·1	29·7	13·0
	L.W.	32·5	12·1	31·8	12·0	23·8	13·2
May 28	H.W.	33·5	13·1	33·4	13·2	28·3	18·0
	L.W.	33·1	14·1	32·5	14·4	21·3	20·0
June 11	H.W.	34·1	14·1	32·0	14·2	30·5	16·0
	L.W.	32·5	16·1	31·8	16·1	28·7	17·5

with high and low water. When samples were not taken on the exact date of springs, they were taken when the tide was still of spring magnitude according to the tide-table.

At a position about half a mile above Hamoaze Buoy No. 15 the following differences in the salinity of the surface layers were noted:

	Salinity ($^{\circ}/_{\circ\circ}$) difference between					
	Surface and 0·9 m.			Surface and 1·8 m.		
Date	Max.	Min.	Mean	Max.	Min.	Mean
May 24	1·9	0·0	0·59 ± 0·22	3·4	0·0	1·55 ± 0·50
June 3	1·1	0·0	0·24 ± 0·14	1·2	0·0	0·41 ± 0·16

These figures are a summary of conditions at hourly intervals from high to low water. It has been pointed out farther back that the data for May 24 may be taken as (roughly) representative of a condition not far short of normal winter condition, and that of June 3 as normal summer. The differences from the surface salinity are small in the first two metres and almost negligible in the first metre. Moreover, the differences between the salinity at the surface and the depths mentioned become less and less on proceeding seaward, till in the Sound, under the worst winter conditions, they are practically non-existent.

Fig. 3 and Table II show the fluctuation in salinity at 6 hr. intervals at each position. There is a fluctuation gradient increasing up-river from the seaward end of the estuary. Not only does the fluctuation increase in range in the up-river direction, but it also moves down in the scale of salinities—both high- and low-water salinities become less (as might be expected) and the low-water salinity decreases to a greater extent than the high-water salinity. The fluctuation is very great at Saltash.

The greatest and least *differences* between the mid-river surface salinity at high water and the succeeding low water are:

	Greatest difference	Least difference
Saltash	12·8$^{\circ}/_{\circ\circ}$ (9·0 atm.)	1·8$^{\circ}/_{\circ\circ}$ (1·5 atm.)
Drake's Island	5·5$^{\circ}/_{\circ\circ}$ (3·5 atm.)	0·2$^{\circ}/_{\circ\circ}$ (—)
Breakwater	5·2$^{\circ}/_{\circ\circ}$ (3·5 atm.)	0·3$^{\circ}/_{\circ\circ}$ (—)

Figures in brackets are the resulting changes of osmotic pressure (corrected for temperature at the prevailing salinities).

The lowest low-water and the highest high-water salinity recorded during January to June, 1937, are ($^{\circ}/_{\circ\circ}$): Saltash, 7·6 and 30·5; Drake's Island, 19·5 and 33·7; and Breakwater, 26·6 and 34·9.

Here we have discussed spring tides as most likely to produce maximum and minimum salinity; but high and low values may sometimes be produced during neaps depending on the rainfall and wind.

October 1936 was an exceptionally dry month and although rainfall increased towards the end of the month it was still below average. During the last week of the month a daily observation of surface salinity at high water and low water was made (Fig. 4) at Weirquay. There is an indication of greater fluctuation at springs than at neaps; and even in dry weather the fluctuation is very great. Fluctuation is greater and has a longer duration of incidence on a buoy than at a corresponding point intertidally (extreme low-water mark excepted).

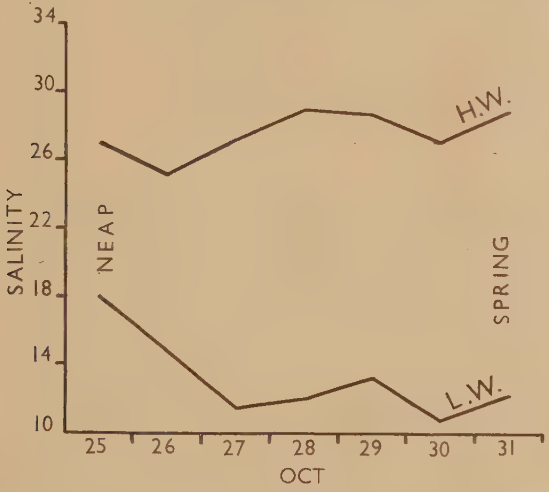


Fig. 4. Daily surface salinity °/₀₀ at high and low water from neap to spring at Weir quay.

The regular sampling of surface salinities was carried out from January to June 1937, but five other spring tide observations were taken during October, November and December 1936 (see Fig. 3).

Rainfall and Salinity

Since rainfall influences salinity, the average total monthly rainfall from October 1936 to September 1937 is also given in Fig. 3. These values have been compiled from data supplied by the Cornwall Rainfall Association from eight stations distributed in the Tamar Valley area. Unfortunately the normal average for the area is available for one only of these eight stations, namely Egloskerry; this, for lack of better, has been included in Fig. 3 as illustrative of the normal average. Rainfall was extraordinarily high in the winter of 1936–7. Mr A. Pearse Jenkin, secretary to the Association, notes that at Redruth in Cornwall the rainfall for the first four months of 1937 was practically equal to the normal fall for the first eight months of the year.

On comparing the rainfall curve with the salinity curves in Fig. 3 it will be seen that there is a noticeable lag between excessive rainfall and salinity depression. That the salinity curves are irregular is explained by the fact that wind and tidal height affect water movement also. For instance at point *X* (Fig. 3) salinity at low water is higher than might be expected taking tidal height and rainfall into account—it ought to have been at least 5°/₀₀ lower. Water movements in the Tamar Estuary are affected by winds from about S.S.W. through S. to S.E. tending to pile water up-river; and winds from the opposite directions tending to push water down-river. At the point *X*, which was on March 19 1937, the Plymouth Meteorological Report gives:

March	Wind direction at 9 a.m.	Velocity at 9 a.m.	Greatest velocity during preceding 24 hr.
18	S.S.W.	25 m.p.h.	49 m.p.h.
19	S.S.W.	18 ,,	45 ,,
20	S.E.	12 ,,	32 ,,

Thus the high salinity recorded at low water was due to the tide being prevented from flowing out to its fullest extent, even though it was a 5 m. tide. The effect of a continued southerly wind is to prevent the ebb flowing completely out of the estuary basin and to pile up the next flow still farther. If river level, tidal height and wind were known, other anomalies could be explained.

OTHER SURFACE AND BOTTOM RECORDS OF SALINITY

Many samples were taken in the estuary of the River Tamar during the course of other work; these are not easily tabulated, but the following is a brief summary, from over 100 records, given in round figures for the sake of clarity; they are included for the use of other workers in this series. When considering mud-dwelling animals, it must be remembered that the salinity of interstitial water is always higher, usually much higher, than that of the overlying water (Tees Survey, 1935; Reid, 1930, 1932). For depths at the various stations see Part I of this series.

Hamoaze near the outlet of St John's Lake (1·5–2 km. from mouth).

In a normal winter the surface salinity at low water varies from 34 to 20°/₀₀; while at high water it varies from 35 to 30°/₀₀. Bottom salinity is generally well over 30°/₀₀ at all states of the tide. In the exceptionally rainy months of January and February 1937, high-water salinities such as 14, 18 and 24°/₀₀ were recorded at the surface. In a normal summer, salinities are not much below open sea condition, and the lowering at low water is naturally much less than in winter.

Saltash (6·8 km. from mouth).

Fig. 3 and Table II give records of surface salinity in all sorts of conditions of spring tide, rainfall and wind, summer and winter. Fig. 1 and Table I, which refer to a station midway between Saltash and Neal Point, gives bottom and intertidal values in what might almost be taken as normal summer and winter conditions. The only other records available for Saltash are bottom salinities for the months of October, November and December of 1936 when the rainfall was only a little below the normal for winter: high water, 30–35$^{\circ}/_{\circ\circ}$; low water, 25–32$^{\circ}/_{\circ\circ}$.

Neal Point (9 km. from mouth).

In a normal winter, surface salinity at low water varies from about 7 to 26$^{\circ}/_{\circ\circ}$; while at high water it ranges from 12 to 29$^{\circ}/_{\circ\circ}$. Bottom salinity is from 24 to 32$^{\circ}/_{\circ\circ}$. Values as low as 4–7$^{\circ}/_{\circ\circ}$ have been recorded for low-water surface in January and February 1937. In a normal summer, high-water surface may be as high as 33$^{\circ}/_{\circ\circ}$.

Weirquay (13 km. from mouth).

In a normal winter, surface salinity at low water may fall to 1$^{\circ}/_{\circ\circ}$, and high water is quite commonly 23$^{\circ}/_{\circ\circ}$. Bottom salinity may be 16–25$^{\circ}/_{\circ\circ}$ at low water, though in excessively rainy periods it will fall much lower. In a normal summer, high-water surface salinity may reach 26$^{\circ}/_{\circ\circ}$.

Pentillie Quay (16·5 km. from mouth).

In a normal winter the surface salinity at low water ranges from less than 1$^{\circ}/_{\circ\circ}$ up to 5$^{\circ}/_{\circ\circ}$; at high water the surface is from 5 to 16$^{\circ}/_{\circ\circ}$. The lowest record from the bottom was 2$^{\circ}/_{\circ\circ}$, though the water may be almost fresh for a short time during a heavy spate. The normal summer surface salinity may reach as high as 24$^{\circ}/_{\circ\circ}$ at high water.

Percival (1929) also gives high-water surface salinities for a dry summer at all these stations.

Attention may here be drawn to the presence of a thin "skin" of practically fresh water on the surface at the upper stations for a short time immediately after an excessive downpour of rain.

Spate waters from the Plym affecting the Sound.

The Plym brings down large quantities of china-clay in colloidal form which give the water a milky appearance. If the wind is from the south, this clay water may be seen on the surface covering an area bounded by a line drawn through the north end of Rum Bay, No. 1 Mooring Buoy Drake's Island, and the bathing pool just below the Laboratory. On January 13 1937, a surface sample just inside this area had a salinity of 16·2$^{\circ}/_{\circ\circ}$ as compared with a salinity of 28·2$^{\circ}/_{\circ\circ}$ on the surface just outside the area (the two sampling stations about 30 m. apart near Drake's Island).

TEMPERATURE OF THE SURFACE WATERS

Morning high-water and afternoon low-water temperatures for springs—at about 8 a.m. and 2 p.m. respectively—were taken fortnightly with standardized thermometers from January to June 1937 at 1 ft. below the surface (0·3 m.) at Saltash, Drake's Island and Breakwater in "mid-river" (Table II); temperatures were also taken at various positions in the open sea beyond the Breakwater. Fig. 5 contains only the Breakwater and Saltash average (between morning and afternoon) temperatures, for the sake of clearness.

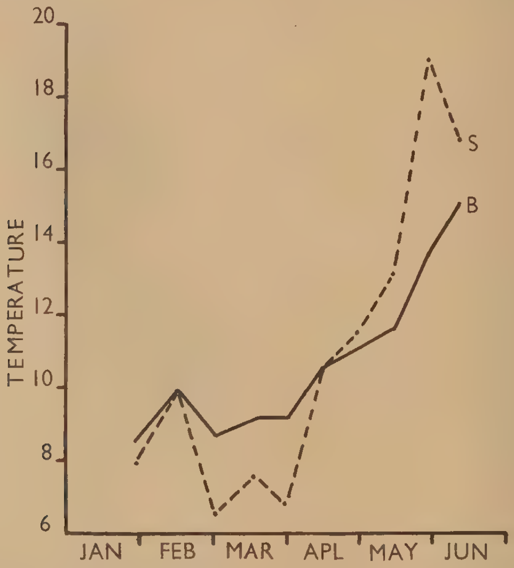


Fig. 5. Temperature (°C.) of surface waters at the Breakwater (*B*) and Saltash (*S*). This is the average between high-water (morning) and low-water (afternoon) temperature at 1 ft. depth (0·3 m.).

In the winter sometimes the morning and sometimes the afternoon temperature was the higher; in the summer the afternoon temperature was always the higher. The differences between morning and afternoon tend to be least at the Breakwater and greatest at Saltash; they vary from 0·0 to 2·0° C., and are greatest in summer.

Temperatures at Saltash were lower in winter and higher in summer than at the Breakwater (Fig. 5). Breakwater temperatures approximate to open sea temperatures; they show only a slight increase in range. Drake's Island records are similar to those at the Breakwater with a small increase in range; the bottom end of the range is lower—showing a decided tendency towards the Saltash condition. Thus we see a gradient from open sea to Saltash, with the smallest range in the former and the greatest in the latter.

The temperature records given are not to be taken as absolute maxima and minima for the period in question; they are intended only as an indication of the conditions prevailing. Maximum ranges recorded were:

Breakwater	8·1–16·1° C.
Drake's Island ...	7·6–16·1° C.
Saltash	6·5–20·0° C.

There must be violent fluctuation in temperature, at least in the marginal waters if not in mid-river, when on a hot day the water runs in over the exposed mud-flats. In mid-river, however, the greatest changes in a fortnight were: Breakwater, 3·0° C., May–June; Drake's Island, 2·9° C., May–June; and Saltash, 7·0° C., May. The temperature increases gradually from winter to summer. Day-to-day fluctuations in temperature were not measured.

Taken alone temperatures may have only a very small effect, but in conjunction with salinity their influence is much increased (cf. Huntsman, 1918) and this combined influence increases in the up-river direction. In estuaries farther north, such as the Dee in Aberdeenshire, very big fluctuations due to the mixture of the relatively warm sea water and large quantities of melted snow may be expected in winter; in such localities, low temperature might be of more importance as a limiting factor than in the Tamar.

Hydrogen-Ion Concentration

The Tamar draws much of its water from peat moor, but sea water is so well buffered that there was little evidence of acidity in the surface waters (at least in that section of the Tamar under consideration) on April 27 1937 when rainfall was of normal winter order, as shown below:

High water at 8 p.m. Samples from 1 ft. depth (0·3 m.). *p*H corrected for salt error.

Position	Time	*p*H	Salinity (°/₀₀)
Pentillie	12 noon	7·54	9·8
Saltash	6.40 p.m.	8·18	29·7
St John's Lake (Hamoaze end)	7.05 p.m.	8·23	32·4
Drake's Island	7.30 p.m.	8·15	33·9

No continuous survey of *p*H was taken.

Thanks are due to Dr H. B. Moore for help in collecting of cross-section samples.

SUMMARY

An attempt has been made to give the range and rate of fluctuation of salinity (and, to a lesser extent, of temperature) that organisms experience at various points on the bed of the lower Tamar Estuary and in the overlying water—especially near the surface. Such work until now does not seem to have been attempted. The following general facts emerge: On proceeding from high-water mark to low-water mark there is an increase in the range, rate and duration of fluctuation in salinity. Also the upper limit of the salinity range rises very slightly while the lower limit falls by a large amount, i.e. there is a more or less uniform gradient from high-water mark to low-water mark. Near high-water mark the fluctuation is less and of shorter incidence and is distributed over a higher level of the total salinity range (for the intertidal area) than near low-water mark. Owing to stratification, the farther down the intertidal area the (slightly) longer is the duration of the high salinities, especially in winter. At mid-tide mark the fluctuation is very similar to that on the bottom in mid-river, but is of twice the rate.

Conditions in the surface waters at 1 ft. depth (0·3 m.), as representative of the top metre at least, were also investigated at fortnightly intervals summer and winter. Samples were taken at springs as being most likely to give an indication of maxima and minima, though wind, tidal height and river level may on occasion combine to give maxima and minima at neaps. As the average salinity decreases up-river the range of fluctuation increases. While both high- and low-water salinities fall, the latter falls more rapidly.

Rainfall in the winter of 1936–7 was exceptionally heavy and there is a noticeable lag between excessive rainfall and depression of salinity.

Rather more scanty data of salinity at various other stations in the region under consideration in this series are given for the use of other workers in the series.

Temperature records for surface waters in summer and winter at springs show that on proceeding up-river (1) there is a slight daily fluctuation in mid-river, (2) there is an increase in the annual range, i.e. the farther from the sea the colder it is in winter and the warmer in summer.

REFERENCES

ALEXANDER, W. B., SOUTHGATE, B. A. & BASSINDALE, R., 1935. Survey of the River Tees. Part II. The Estuary—chemical and biological. *D.S.I.R. Water Pollution Research*, Tech. Paper No. 5, H.M. Stationery Office.

HARTLEY, P. H. T. & SPOONER, G. M., 1938. The ecology of the Tamar Estuary. I. Introduction. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 501–8.

HUNTSMAN, A. G., 1918. The vertical distribution of certain intertidal animals. *Trans. Roy. Soc. Canada*, Sect. IV, p. 53.

PERCIVAL, E., 1929. A Report on the fauna of the estuaries of the River Tamar and River Lynher. *Journ. Mar. Biol. Assoc.*, Vol. XVI, p. 81.

REID, D. M., 1930. Salinity interchange between sea water in sand and overflowing fresh water at low-tide. *Journ. Mar. Biol. Assoc.*, Vol. XVI, p. 609.

—— 1932. Salinity interchange between sea water in sand and overflowing fresh water at low-tide. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, p. 299.

CAMBRIDGE: PRINTED BY W. LEWIS, M.A., AT THE UNIVERSITY PRESS

INDEX

A
Acabaria pulchra, preservation of, 296, 297, 298
Acanthochiton spinigera, preservation of, 296, 297
Acartia, as food of herring larvae, 253, 260
Acmaea rubella, viviparity in, 119
Actinia quadricolor, preservation of, 297, 298
Aeolidia papillosa, metallic constituents of, 270
Aeolis, preservation of, 296, 297
Aequorea forskalea, seasonal distribution, 413, 416, 417
— *vitrina*, 412; seasonal distribution, 413, 416, 417
Agastra mira, seasonal distribution, 413, 416
Aglantha digitalis, 435
— *rosea*, seasonal distribution, 413, 416, 417, 433
Aglaura hemistoma, 414
Agonus cataphractus, vertebral characters, 46
Alcyonium, preservation of, 298
Alosa alosa, number of vertebrae, 23, 36, 38
Alvania cimicoides, 131, 132
— *crassa*, 113, 131
— *jeffreysii*, 132
— *punctura*, 112, 113, 130, 132
Ammodytes, function of vertebrae, 5, 10, number, 23, 43, 44; seasonal abundance of post-larvae, 500
Amphinema, identity of species, 61
— *apicatum*, 71
— *dinema*, rearing hydroids of, 62, 64, 70, 81, 384; seasonal distribution, 413, 416, 420; identification of, 424
— *rugosum*, rearing hydroids of, 67, 69; seasonal distribution, 413, 416, 417, 420; biology of, 424
Anarhichas lupus, structure of vertebrae, 12, 43–5
Anguilla, structure of vertebrae, 12, 51
Angustispira spengeli, 141
Aplysia punctata, metallic constituents of, 270
Aporrhais pespelicani, eggs, 112, 113, 144; ciliary currents in, 454, 462, 466
Arca, ciliary feeding in, 465
Archidoris britannica, metallic constituents of, 269, 271, 273
Argentina silus, number of vertebrae, 23, 24
Argyropelecus olfersi, 20
Arnoglossus, function of vertebrae, 11, 13; number, 23, 47, 49; seasonal abundance of post-larvae, 493, 494, 500
Arsenia punctura, 132
Asterias vulgaris, 345, 353
Asteronotus hemprichi, preservation of, 296
Astroboa, preservation of, 297
Atherina presbyter, number of vertebrae, 23, 43
Aurelia aurita, 416

B
Bacteria, relation of, to diatoms in seawater, 359
Balanus, 507
Balcis alba, larvae of, 107, 112, 113, 140
— *devians*, larval form, 113, 140
Balistes capriscus, function of vertebrae, 9, 54
Barleeia unifasciata, larvae of, 107, 113; eggs, 112, 134
Bela trevelyana, 158
Belone belone, structure of vertebrae, 53
Beringius turtoni, larval form, 116, 154
Biddulphia mobiliensis, iron in, 210, 213; compensation point, 336; growth rate, 381
— *regia*, 311, 338
— *sinensis*, iron in, 213
Bittium reticulatum, eggs, 112; larval form, 113, 137
Blennius, structure of vertebrae, 12, 43, 45; seasonal abundance, 493, 500
Bougainvillia britannica, 80; seasonal distribution, 413, 416, 420; biology of, 421
— *fruticosa*, 80
— *muscus*, 80
— *principis*, seasonal distribution, 413, 416, 417; rarity of, at Plymouth, 423
— *pyramidata*, 414
— *ramosa*, seasonal distribution, 413, 416, 417
Box, structure of vertebrae, 12, 42
Branchiomma vesiculosum, metamorphosis, 228
Buccinopsis dalei, 154
Buccinum humphreysianum, larval form, 116, 156
— *ovum*, 154
— *undatum*, 107, 116, 152, 156; metallic constituents of, 270; ciliary currents in, 453, 455, 462

C
Caecum imperforatum, larval form, 113, 136
Calanus finmarchicus, selective feeding by, 97; as food of larval herring, 253, 257, 260

Calliactis polypus, preservation of, 298
Callionymus, structure of vertebrae, 9; seasonal abundance of young, 494, 500
Calliostoma, larvae of, 108, 110, 120
— *papillosum*, 110, 121
— *zizyphinum*, 110, 121
Calyptraea chinensis, eggs, 113; larval form, 113, 143, 144; feeding mechanism in, 455, 457
Cantharidus, eggs and larvae of, 108, 110, 120, 123
— *clelandi*, 123
— *exasperatus*, 110, 123
— *montagui*, 123
— *striatus*, 110, 123
Cantharus, structure of vertebrae, 12, 42
Capros aper, function of vertebrae, 9, 50; seasonal abundance of post-larvae, 500
Capulus ungaricus, larva, 106, 113; eggs, 113, 143; ciliary feeding in, 453, 455, 459, 462
Caranx trachurus, structure of vertebrae, 7–9, 23, 30, 42, 43; seasonal abundance of post-larvae, 493, 500
Cardium edule, metallic constituents of, 270; rearing of, 383; shells in mud deposits, 505
— *nodosum*, rearing of, 383
Caridion gordoni, 102
— *steveni*, 102
Centrolabrus exoletus, number of vertebrae, 23, 43
Centropages, as food of herring larvae, 253, 260
Cepola rubescens, number of vertebrae, 23, 42, 43; fat content, 389; seasonal abundance of post-larvae, 500
Cerithiopsis, larvae of, 107
— *barleei*, eggs, 112; larval form, 113, 138
— *jeffreysi*, 138
— *tubercularis*, eggs, 112; larval form, 113, 137
Chaetoceros, relation of bacteria to, 366
— *pseudocurvisetus*, iron in, 212, 214
Chauvetia brunnea, 156
Chilodactylus, structure of vertebrae, 44
Chirolophis galerita, 500
Chironemus, structure of vertebrae, 44
Chromodoris annulata, preservation of, 297
Chrysallida decussata, eggs, 112, 141
Chrysaora isosceles, 416
Cingula (*Anoba*) *semicostata*, 107
— *cingillus*, eggs and young, 107, 112, 113, 131
— *fulgida*, eggs, 112; larval form, 113, 130
— *semicostata*, eggs and young, 112, 113, 129, 130
— *semistriata*, 112, 113, 131
Cirrhites, structure of vertebrae, 44
Cladocera, as food of herring larvae, 253
Clathraria rubinoides, preservation of, 296
Clathrus clathrus, eggs, 113, 139
Clavularia, preservation of, 296, 298
Clupea harengus, structure of vertebrae, 7, 23, 26, 28, 38; seasonal abundance of post-larvae, 500
— *pilchardus*, 498
— *sprattus*, number of vertebrae, 23, 24, 26, 38
Clytia johnstoni, 430
Colus gracilis, larval form, 116, 155
— *howsei*, 116, 155
— *islandicus*, 116, 155
— *jeffreysianus*, 155
Conger, structure of vertebrae, 6, 12, 51, 53
Contractile marine animals, preservation of, 295
Coris cuvieri, structure of vertebrae, 44
Corymorpha nutans, rearing of, 384
Coscinodiscus excentricus, oxygen production by, 301; phosphorus and nitrogen in, 342
Coscinoscira polychorda, 339
Cosmetira megalotis, 428
— *pilosella*, 76, 428; seasonal distribution, 413, 415, 416, 417
Cottus, seasonal abundance of post-larvae, 500
— *bubalis*, vertebral characters, 46
Crangon vulgaris, food of flounders, 390
Crenilabrus melops, form of backbone, 43; post-larvae, 500
Crepidula fornicata, eggs, 113, 143, 144; ciliary feeding mechanism in, 455, 457, 462
Ctenolabrus rupestris, number of vertebrae, 23, 43; seasonal abundance of post-larvae, 493, 500
Cucumaria lactea, tube feet of, 345, 349, 351, 353
Cuspidella, 75
— *costata*, 76
— *grandis*, 76
— *humilis*, 76
Cyanea lamarcki, 416

D

Defrancia reticulata, 161
Diatoms, size-changes of, 83; supply of iron to, 205; oxygen production by, 301; relation of bacteria to, 359
Dichelopandalus leptoceros, 102
Didymozoon auxis, 491
— *faciale*, sp.n., 486
— *minor*, 491
— *scombri*, 485, 487
— *sphyraenae*, 491

Diodora, eggs and larvae of, 108, 110
— *apertura*, 110, 117
Dipleurosoma typicum, 414
Dipurena halterata, seasonal distribution, 413, 416, 417
Discomedusa lobata, at Plymouth, 412, 416, 417, 497
Discosoma giganteum, 298
Ditylium brightwellii, 98
Doliolum gegenbauri, 420
Doridopsis nigra, preservation of, 296, 297
Dreissensia polymorpha, 471

E

Echinoderms, structure and function of tube feet in, 345
Echinus esculentus, tube feet of, 345, 349, 351
Ectopleura dumortieri, seasonal distribution, 413, 417
Eirene viridula, seasonal distribution, 413, 416, 420, 432
Engraulis, function of vertebrae, 6, number, 23, 38
Ensis siliqua, rearing of, 384
Erato laevis, 150
— *voluta*, larval form, 113, 150, 228
Eucheilota, 384
— *clausa*, 412; seasonal distribution, 413, 414, 416, 418, 432
Eucodonium brownei, seasonal distribution, 413, 416
Eudendrium pudicum, 74
Eulima alba, 140
— *distorta*, 140
— *philippi*, 140
Eunicella verrucosa, 64, 71, 80
Euphysa aurata, seasonal distribution, 413, 416, 417
Eurytemora hirundinoides, 260
Eutima insignis, seasonal distribution, 413, 418

F

Favia, preservation of, 296
Fishes, vertebral variation in teleostean, 1, 387; estimation of age from bony structures, 21; sense organs, 385; seasonal abundance of pelagic stages, 388, 493; fat content, 388; behaviour experiments, 390
Fishing nets, preservation of, 390
Fissurella nubecula, eggs of, 117
Fungia, preservation of, 296, 298
Fusus antiquus, 155
— *buccinatus*, 155
— *gracilis*, 155
— *propinquus*, 155

G

Gadopsis, structure of vertebrae, 44
Gadus, form and function of vertebrae, 5, 14; number of vertebrae, 23, 24, 26, 40; seasonal abundance of young, 494, 500
Galeomma turtoni, 448
Gammarus chevreuxi, researches on, 386
— *zaddachi*, 507
Gibbula, eggs and larvae, 107, 108, 110, 120, 122
— *cineraria*, 122
— *cinerarius*, 107
— *magus*, 110
— *obliquatus*, 122
— *tumida*, 110, 120, 122
— *umbilicalis*, 107, 110, 122
Glossodoris quadricolor, preservation of, 297
Glycymeris, ciliary feeding in, 465
Gobius, seasonal abundance of young, 494, 500
Goniopora columna, preservation of, 296, 298
Gossea corynetes, 412; seasonal distribution, 413, 416

H

Haedroplura septangularis, 159
Haliotis tuberculata, eggs and larvae of, 110, 117
Haplodactylus, structure of vertebrae, 44
Helgicirrha schulzei, 412; seasonal distribution, 413, 414, 416, 432
Herring, growth and feeding of Clyde, 245; comparison of food and plankton, 258; chemical composition, 281; driftnet fishery at Plymouth, 387; seasonal abundance of post-larvae, 500
Hexabranchus sanguineus, preservation of, 296, 297
Hippoglossoides platessoides, number of vertebrae, 23
Hippoglossus, number of vertebrae, 49
Hybocodon prolifer, seasonal distribution, 413, 416
Hydrobia jenkinsi, see *Errata*
— *ulvae*, 112, 113, 128, 129
— *ventrosa*, 112, 128, 129 (see *Errata*)
Hydroids, methods of rearing, 77

I

Ianthina britannica, 139

J

Jorunna tormentosa, metallic constituents of, 269
Julis pavo, structure of vertebrae, 44

K

Katsuwonus, function of vertebrae, 8, 12, 43
Kellia suborbicularis, rearing of, 384; life history, 447

L

Labrus, structure of vertebrae, 9, 10, 43; sexual dimorphism, 16; estimation of age, 21; seasonal abundance of post-larvae, 500
Lacuna divaricata, 125
— *pallidula*, eggs and larvae, 107, 112, 113, 125, 126
— *parva*, 125
— *puteolus*, 125
— *vincta*, eggs and larvae, 107, 112, 125; metallic constituents of, 269, 271
Lamellaria latens, 113, 149
— *perspicua*, eggs and larval form, 113, 148
Lamellariidae, classification, 147
Laodicea undulata, hydroid of, 76; rearing, 80; seasonal distribution, 413, 416, 417, 427
Lasaea rubra, 448
Latreutes fucorum, 102
Latris, structure of vertebrae, 44
Lauderia borealis, 98; iron in, 210
Lepidorhombus whiffiagonis, number of vertebrae, 23, 47
Leuckartiara, 70
— *breviconis*, 414
— *nobilis*, 414
— *octona*, seasonal distribution, 413, 416
Lima, rearing of, 384
Limacina turritelloides, 138
Liomesus ovum, 154
Liriope exigua, seasonal distribution, 413, 416, 417
Littorina, eggs and larvae of, 107, 110
— *littoralis*, 107, 112, 113, 126, 128; metallic constituents of, 270
— *littorea*, 107, 110, 112, 113, 126, 127, 507; metallic constituents of, 269; ciliary currents in, 455; shells in mud flats, 504
— *neritoides*, 107, 112, 128; metallic constituents of, 269
— *obtusata*, 107, 126
— *rudis*, 107, 126; metallic constituents of, 269; ciliary currents in, 455, 462
— *saxatilis*, 107, 112, 126
Lizzia blondina, rearing hydroids of, 80; seasonal distribution, 413, 416, 418
Lobophytum, preservation of, 298
Lophius piscatorius, structure of vertebrae, 56; habits, 389; seasonal abundance of post-larvae, 500
Lora trevelliana, 158
— *turricula*, larval form, 116, 159
Lovenella clausa, 384

M

Mackerel, biology of, 388
Mangelia coarctata, 159
— *nebula*, larval form, 116, 159
Margarites groenlandicus, eggs and larvae, 121
— *helicinus*, eggs and larvae, 110, 121
Marthasterias glacialis, tube feet of, 345, 349, 351, 353
Medusae, rearing hydroids of, 77; Plymouth offshore, 411
Melicertum octocostatum, 415
Merluccius merluccius, structure of vertebrae, 7, 39; seasonal abundance of post-larvae, 500
Microcalanus, as food of herring larvae, 253, 257, 260
Mitrocomella brownei, 61; rearing hydroids of, 75, 80; seasonal distribution, 413, 416, 418
— *fulva*, seasonal distribution, 413, 416
Mola mola, structure of vertebrae, 55
Molva elongata, number of vertebrae, 23
— *molva*, function of vertebrae, 20, number, 23; seasonal abundance of post-larvae, 500
Monodonta lineata, eggs and larvae of, 107, 108, 110, 120, 123
Montacuta bidentata, 447
— *ferruginosa*, 447
Mora, growth rings, 21; number of vertebrae, 23
Morone labrax, structure of vertebrae, 6; estimation of age, 21; number of vertebrae, 23, 32, 42; seasonal abundance of post-larvae, 500
Muggiaea atlantica, 383, 416, 417; development of, 441; abundance of, 497
— *kochi*, 383, 412, 416, 417, 441, 445, 497
Mugil, structure of vertebrae, 9, 12; estimation of age, 21; number of vertebrae, 33, 43, 45
Mullus, structure of vertebrae, 9, 23, number, 32, 42; seasonal abundance of post-larvae, 500
Mysella bidentata, 447
Mytilus edulis, metallic constituents of, 270; development of, 472

N

Nassarius incrassatus, larvae of, 107, 116, 146, 157, 228
— *pygmaeus*, larval form, 116, 158
— *reticulatus*, larvae of, 107, 116, 146, 157, 228; ciliary currents in, 455
Natica alderi, 146
— *catena*, eggs, 113; larva, 145, 228
— *groenlandica*, 145
— *maculata*, 145, 228
— *millipunctata*, 145
— *pallida*, 146
— *poliana*, eggs, 113, 145
— *pulchella*, 146

Nematobothrium filarina, 491
Neptunia antiqua, larval form, 116, 155
Nitrogen, ratio of, to phosphorus in the sea, 177; cycle of, in the sea, 183
Nitzschia closterium, food of *Calanus finmarchicus*, 97; iron in, 214; relation of bacteria to, 363, 366
Notomastus latericeus, influence of substratum on development, 227
Nucella lapillus, 107, 116, eggs and larvae, 153; metallic constituents of, 269; ciliary currents in, 455

O

Obelia, seasonal distribution, 413, 416, 432
Obituary: E. T. Browne, 405
Ocenebra erinacea, larval form, 116, 153
Octorchis gegenbauri, rearing of, 80, 384; seasonal distribution, 413, 416
Odax richardsoni, structure of vertebrae, 44
Odostomia eulimoides, 112, 113, 142
— *tellinae*, 141
Oithona, as food of herring larvae, 253, 257, 260
Omalogyra atomus, 112, 135
Oncidium, preservation of, 296, 297
Onos, structure of vertebrae, 11, 40; seasonal abundance of young, 494, 500
— *mustelus*, number of vertebrae, 23
Ophiocomina nigra, tube feet of, 345, 348, 355
Ophionereis reticulata, tube feet of, 354
Ophiothrix fragilis, tube feet of, 345, 346, 356
Ophiura brevispina, 354
— *texturata*, tube feet of, 345, 349, 354
Ostrea chilensis, 478
— *commercialis*, 469, 480
— *cucullata*, 478
— *edulis*, metallic constituents of, 270; metamorphosis, 469
— *gigas*, 470
— *lurida*, 470, 479, 480
— *virginica*, metamorphosis, 469, 475, 479
Owenia fusiformis, metamorphosis, 228, 241
Oxygen production by *Coscinodiscus*, 301

P

Pagellus, structure of vertebrae, 12, 42
Palythoa tuberculata, preservation of, 298
Paractis adherens, 298
— *hemprichi*, 298
Patella, eggs of, 107, 108, 110, 118
— *athletica*, 118
— *cerulea*, 118
— *depressa*, 118
— *intermedia*, 118
— *vulgata*, 118
Patelloida tessullata, eggs and larvae, 119
— *virginea*, eggs and larvae, 110, 119
Patina, eggs and larvae of, 108, 110
— *pellucida*, 119
Pecten maximus, metallic constituents of, 270
Pelagia noctiluca, at Plymouth, 412, 416, 417, 497
Pelseneeria stylifera, eggs, 112; larval form, 113, 141
Perigonimus muscoides, 70
— *nutans*, 71
— *quadritentaculatus*, 74
— *repens*, 70
— *serpens*, 64, 66, 69; on *Plumularia setacea*, 69; on *Cellaria fistulosa* and *Gorgonia* sp., 70
Peringia ulvae, shells in mud flats, 504
Phialella cymbaloides, 80; seasonal distribution, 413, 416, 418
Phialidium hemisphericum, 80; seasonal distribution, 413, 416, 418, 429; observations on, 429
Philbertia asperrima, 161
— *gracilis*, larval form, 116, 159, 160, 228
— *leufroyi*, 116, 161
— *linearis*, 116, 159, 161, 228
— *purpurea*, 161
— *teres*, 162
Pholis gunnellus, structure of vertebrae, 12, 43
Photo-electric measurement of illumination, 379, 509
Photosynthesis, 311
Phrynorhombus, number of vertebrae, 23, 47
Plankton, ratio of nitrogen to phosphorus in, 177; as food of herring larvae, 253; chemical composition of, 382; indicators, 415, 495, 497
Pleurobranchus delicatus, preservation of, 296
Pleuronectes, number of vertebrae, 23, 26, 49
— *cynoglossus*, 23, 49
— *flesus*, 23, 49, 500
— *limanda*, 23, 49; seasonal abundance of young, 494, 500
— *microcephalus*, function of vertebrae, 12; seasonal abundance of young, 494, 500
— *platessa*, 23, 49
Pochella polynema, 412; seasonal distribution, 413, 414, 416; biology of, 425
Podocoryne areolata, seasonal distribution, 413, 416, 417
— *carnea*, seasonal distribution, 413, 416, 417
Proboscidactyla polynema, 427
Prosobranchs, eggs and larvae of British, 105
Psammechinus miliaris, 141
Psettodes erumei, number of vertebrae, 47
Pseudocalanus, as food of herring larvae, 253, 257, 260

Pterocera, evolution of ciliary feeding, 455
Purena gemmifera, seasonal distribution, 413, 416, 418, 420
— *strangulata*, seasonal distribution, 413, 416, 417
Purpura lapillus, 385
Pyrgulina decussata, 141

R

Raniceps raninus, structure of vertebrae, 7, 41; seasonal abundance of post-larvae, 500
Rathkea octopunctata, 61; rearing hydroids of, 71, 80; seasonal distribution, 413, 416, 418
Rays, migrations and growth of, 387
Reinhardtius, number of vertebrae, 49
Remora remora, structure of vertebrae, 9, 54
Report of Council, 1936, 375
Rhincalanus nasutus, at Plymouth, 497
Rhizosolenia, relation of bacteria to, 360, 366
— *styliformis*, populations of, 83, 93, 95
Rhombus maximus, number of vertebrae, 23, 47, 50; seasonal abundance of post-larvae, 500
Rhopalonema coeruleum, 414
Rissoa albella, 132
— *costata*, 130
— *guerini*, 134
— *inconspicua*, 133
— *membranacea*, 130, 134
— *octona*, 130
— *parva*, 130, 133, 134, 228
— *sarsii*, 130, 131, 132, 133
Rissoella diaphana, eggs, 112; larval form, 113, 135
— *opalina*, 136

S

Sagitta elegans, 178, 382, 415, 420, 495, 498
— *setosa*, 178, 383, 415, 495, 498
Salicornia, 503
Salmo trutta, number of vertebrae, 23
Salpa fusiformis, 497
— *mucronata*, 420
Saphenia gracilis, seasonal distribution, 413, 416, 418
Sarcophytum, preservation of, 298
Sardina pilchardus, number of vertebrae, 23, 24, 38
Sarsia eximia, seasonal distribution, 413, 416, 417
— *prolifer*, seasonal distribution, 413, 416
— *tubulosa*, seasonal distribution, 413, 416, 417
Scaphander lignarius, metallic constituents of, 269, 270
Scarus aurofrontus, structure of vertebrae, 44
Scolecolepis fuliginosa, metamorphosis, 228, 242
Scomber, function of vertebrae, 6, 8, 12, number, 23, 29, 42–4; trematodes in, 485; seasonal abundance of post-larvae, 493, 494, 500
Scombresox saurus, structure of vertebrae, 53
Scophthalmus norvegicus, seasonal abundance, 494, 500
Scorpaena, structure of vertebrae, 7, 19, 23, number, 33, 45
Scrobicularia plana, shells in mud flats, 504
Sea water, oxidation-reduction potential in, 167, 380; ratio of nitrogen to phosphorus in, 177, 380; colloidal ferric hydroxide in, 221, 380; illumination in, 509
Sebastes, structure of vertebrae, 6, 19, 45
Serranus, structure of vertebrae, 9; estimation of age, 21; number of vertebrae, 23, 42, 45; seasonal abundance of young, 494, 500
Simnia patula, eggs, 112, 151; larval form, 113, 151
Sinusigera dautzenbergi, 138
— *perversa*, 138
Skeletonema, relation of bacteria to, 366
Skenea serpuloides, eggs and larvae of, 110, 124
Skeneopsis planorbis, eggs, 112; larval form, 113, 135
Solea, function of vertebrae, 11, number, 23, 26, 47; seasonal abundance of young, 494, 500
Solmaris corona, seasonal distribution, 413, 416, 417
Sphaerostoma hombergi, metallic constituents of, 270
Spirographis spallanzani, food of dabs, 390
Spirontocaris cranchii, 101
— *gaimardi*, 102
— *groenlandica*, 102
— *occulta*, 101
— *polaris*, 101
— *pusiola*, 101
— *spinus* var. *lilljeborgi*, larva of, 101
Stauridium productum, 385
Staurocoryne filiformis, 385
Steenstrupia nutans, seasonal distribution, 413, 416, 420
— *rubra*, 80
Sternoptyx diaphana, 20
Stilifer stylifer, 141
Stomotoca apicata, 62
— *rugosa*, 61
Submarine illumination, 303
Substratum, influence of, on larval metamorphosis, 227
Sympodium, preservation of, 296–8
Syntagma brunnea, 156

T
Tamar Estuary, ecology of, 501, 509, 529
Temora, as food of herring larvae, 253, 260
Thalassianthus aster, 297, 298
Thalassiosira gravida, iron in, 213
Thordisa crosslandi, preservation of, 296
Tiaropsis multicirrata, seasonal distribution, 413, 416, 417, 429
Tornus subcarinatus, larval form, 113, 134
Trachinus vipera, number of vertebrae, 43, 44; seasonal abundance of post-larvae, 500
Trichotropis borealis, 142
— *conica*, 142
Trichydra pudica, 71, 74
Tricolia, 110, 124
Trigla, structure of vertebrae, 6, 12, 46; seasonal abundance of post-larvae, 500
Triphora perversa, 107; eggs, 112, 113, 138, 141
Tritonium ovum, 154
Trivia arctica, 107, 113, 149, 151
— *europea*, 150
— *monacha*, 107, 113, 149, 150
Trochus conuloides, 121
— *granulatus*, 121
— *niloticus*, development of, 120
— (*zizyphinus*) *milligranus*, 123
Trophon muricatus, larval form, 116, 152
Tubipora musica, preservation of, 296, 298
Tuck-net fishing, 390
Turbinaria mesentrina, preservation of, 296
Turbonilla elegantissima, larvae, 142
— *fenestrata*, 142
— *lactea*, 142
Turritella communis, eggs, 112; larval form, 113, 136; ciliary feeding in, 468
Turritopsis nutricula, 80, 384, 412, 413, 414, 416, 417, 423
Turtonia minuta, 448

U
Urophycis blennoides, structure of vertebrae, 7, number, 23, 41
Urosalpinx cinerea, larval form, 116, 153

V
Velutina undata, 148
— *velutina*, larvae, 113, 148
Vermetus gigas, mode of feeding, 456, 465, 466
— *novae-hollandiae*, ciliary feeding mechanism in, 455, 456, 462, 466
Vesicularia marina, 156
Volutopsius norwegicus, larval form, 116, 154

W
Wedlia bipartita, 490
Willia stellata, seasonal distribution, 413, 416

Z
Zanclea costata, seasonal distribution, 413, 417; biology of, 420
— *implexa*, 384
Zeugopterus punctatus, number of vertebrae, 23, 47; seasonal abundance of post-larvae, 500
— *unimaculatus*, 500
Zeus faber, structure of vertebrae, 9, 50, 54; estimation of age, 21; seasonal abundance of post-larvae, 500

CAMBRIDGE: PRINTED BY W. LEWIS, M.A., AT THE UNIVERSITY PRESS

Oahu Pr

APR 1956
LIBRARY
POFI
FISH & WILDLIFE
SERVICE